

LOWER CARBONIFEROUS MICROFLORAS OF SPITSBERGEN

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ABSTRACT. Dispersed microspores recovered from the Culm succession (Lower Carboniferous) of Spitsbergen are described in detail and an assessment is made of their value in the elucidation of problems of stratigraphical correlation. The majority of the samples studied are from the Billefjorden Sandstones (i.e. the Culm sequence of Central Vestspitsbergen), which consist typically of sandstones, together with subordinate carbonaceous shales and siltstones and minor coal seams. Detailed collections from three of the most complete sections of the Billefjorden Sandstones, at Birger Johnsonfjellet, Triungen, and Citadellet, present a comprehensive picture of the microfloral succession. As such, they serve as valuable local reference columns with which numerous additional samples, from a variety of localities and horizons in Spitsbergen and Bjørnøya, may be correlated upon microfloral evidence. Two distinct, successive, microfloral assemblages are distinguishable within the otherwise sparsely fossiliferous Billefjorden Sandstones. The presence of numerous species recorded previously from various horizons of the Russian Lower Carboniferous and of the Mississippian of Canada facilitates international correlation. In terms of the standard European stages, the age of the Billefjorden Sandstones is shown to range from Tournaisian to Upper Viséan or lowest Namurian; in terms of North American (Mississippian) nomenclature, the series ranges in age from Kinderhook to lower or middle Chester. This paper includes the systematic descriptions of 115 microspore species. One new genus (*Radialetes*) and thirty-nine new species are proposed. Another genus (*Diatomozonotriletes*) is validated and emended. Three probably new species are described but not specifically named due to their insufficient representation. The remaining seventy-three species are all referable to previously described types. Consideration is given to relevant problems in dispersed-spore taxonomy, botanical relationships, and to differences in microspore composition of various lithological types.

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PART ONE

In October 1958 the writer commenced a study, at the Sedgwick Museum, Cambridge, of the spores contained in samples from the Culm succession (Lower Carboniferous) of Spitsbergen. This research was undertaken at the joint suggestion of Messrs. N. F. Hughes and W. B. Harland. An initial palynological study by Mr. Hughes and Mrs. Margaret Mortimer of some samples then available had disclosed the presence of prolific microfloras of potential stratigraphical value.

A preliminary paper (Hughes and Playford 1961) incorporated early results of the investigation; it was based upon the microfloral study of three representative samples of the Billefjorden Sandstones, which is the name given to the Culm development in Central Vestspitsbergen (Forbes, Harland, and Hughes 1958). One of the samples (B685), a sandstone from Citadellet, contained a diverse and well-preserved microflora which suggested a Tournaisian age; corroborative spore evidence for such an age is provided by numerous other samples, recorded herein, from Citadellet and from other localities. The other two samples, S59a (from the north side of Wordiekammen) and B609 (from the south side of Ebbadalén), contained a different and demonstratively younger (Viséan or lowest Namurian) microflora, which is represented in the majority of samples examined subsequently by the present writer.

The large bulk of the samples upon which the present study is based had been col-

lected by members of Cambridge Spitsbergen Expeditions organized from the Sedgwick Museum. In particular, the detailed collections made in 1959 from the Billefjorden Sandstones have proved especially valuable. The purpose of this study was twofold. Firstly, to describe systematically the microspores present in the Culm succession of Spitsbergen. Secondly, to assess the correlative value of the microfloras, both within and outside Spitsbergen. As will be shown subsequently, external correlation of the Billefjorden Sandstones is facilitated by the close similarity of the microfloras contained therein, with previously described microfloras from the Lower Carboniferous of the U.S.S.R. and from certain horizons of the Canadian Mississippian. Hence, on the basis of microfloral evidence, dating of the Spitsbergen Culm with reference to the standard European Lower Carboniferous stages is a necessarily indirect process, since no spore floras have yet been recorded from the type areas of these stages. Thus, where 'Tournaisian', 'Viséan', and 'Upper Viséan/lowest Namurian' are specified herein with regard to the age of the Spitsbergen Culm, it is emphasized that their validity in that context is dependent directly upon the precision with which the Russian and Canadian sequences may be correlated with that of north-western Europe. This subject will be discussed more fully subsequently. It is important to note here that as a result of recommendations accepted at the XXIst International Geological Congress (*vide* Mr. W. B. Harland) it is likely that the terms 'Lower', 'Middle', and 'Upper' Carboniferous will in the future be used only with reference to the Russian succession; and furthermore that new stage names (presumably approximate equivalents of Tournaisian, Viséan, and Namurian A-B) are expected to be proposed by Russian stratigraphers for the subdivisions of their Lower Carboniferous. In the western European Carboniferous, the names 'Dinantian' and 'Silesian' are to be used as the two primary subdivisions of the Carboniferous; the former including the Tournaisian and Viséan, and the latter including the Namurian, Westphalian, and Stephanian. The Mississippian and Pennsylvanian nomenclature as applied to the North American succession is to remain unchanged. These proposals have obvious relevance in connexion with the international correlation of the Spitsbergen Culm, but have not as yet been detailed in publication. For the present purpose, the term 'Lower Carboniferous' is conveniently used in a general sense to embrace Tournaisian, Viséan, and Lower Namurian, corresponding thus approximately to 'Mississippian', and to its Scottish connotation.

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STRATIGRAPHY

The Lower Carboniferous (Culm) succession of Spitsbergen consists principally of sandstones, together with carbonaceous shales and siltstones and minor lenses of coal. It represents a typical non-marine (deltaic and lacustrine) sequence, showing marked local changes in thickness and notable lateral and vertical lithological variation. The formation rests unconformably upon folded Middle Devonian or older rocks, and (in Central Vestspitsbergen) passes upwards by concordant transition into the Lower Gypsiferous Series, the lower unit of the Campbellryggen Group which is considered to be of Middle Carboniferous age (Gee, Harland, and McWhae 1952, p. 342; Forbes, Harland, and Hughes 1958, p. 486).

The term 'Culm' has been consistently applied (Nathorst 1910, Orvin 1940, Gee *et al.* 1952, and others) to the Lower Carboniferous continental succession of Svalbard, despite the fact that the deposits are quite dissimilar from the typical Culm (Kulm) deep-water facies of south-west England and Germany. More recently, Forbes *et al.* (1958) proposed the name Billefjorden Sandstones for the characteristic development, in Central Vestspitsbergen, of this distinctive plant-bearing series, whilst retaining Culm 'for general use in Svalbard in the sense of Nathorst 1910'.

Plant macrofossils occur at many horizons and have been generally regarded as indicative of a Lower Carboniferous age. As listed by Forbes *et al.* (1958, pp. 468-9), the macroflora of the Billefjorden Sandstones consists predominantly of representatives of *Lepidodendron* and of the Sublepidodendron group, together with some macrophyllous leaves (*Cardiopteridium*, *Sphenopteridium*, *Adiantites*) which are probably mostly pteridospermous. On the basis of this palaeontological evidence Forbes and his co-authors concluded that sedimentation occurred during a large portion of Lower Carboniferous time.

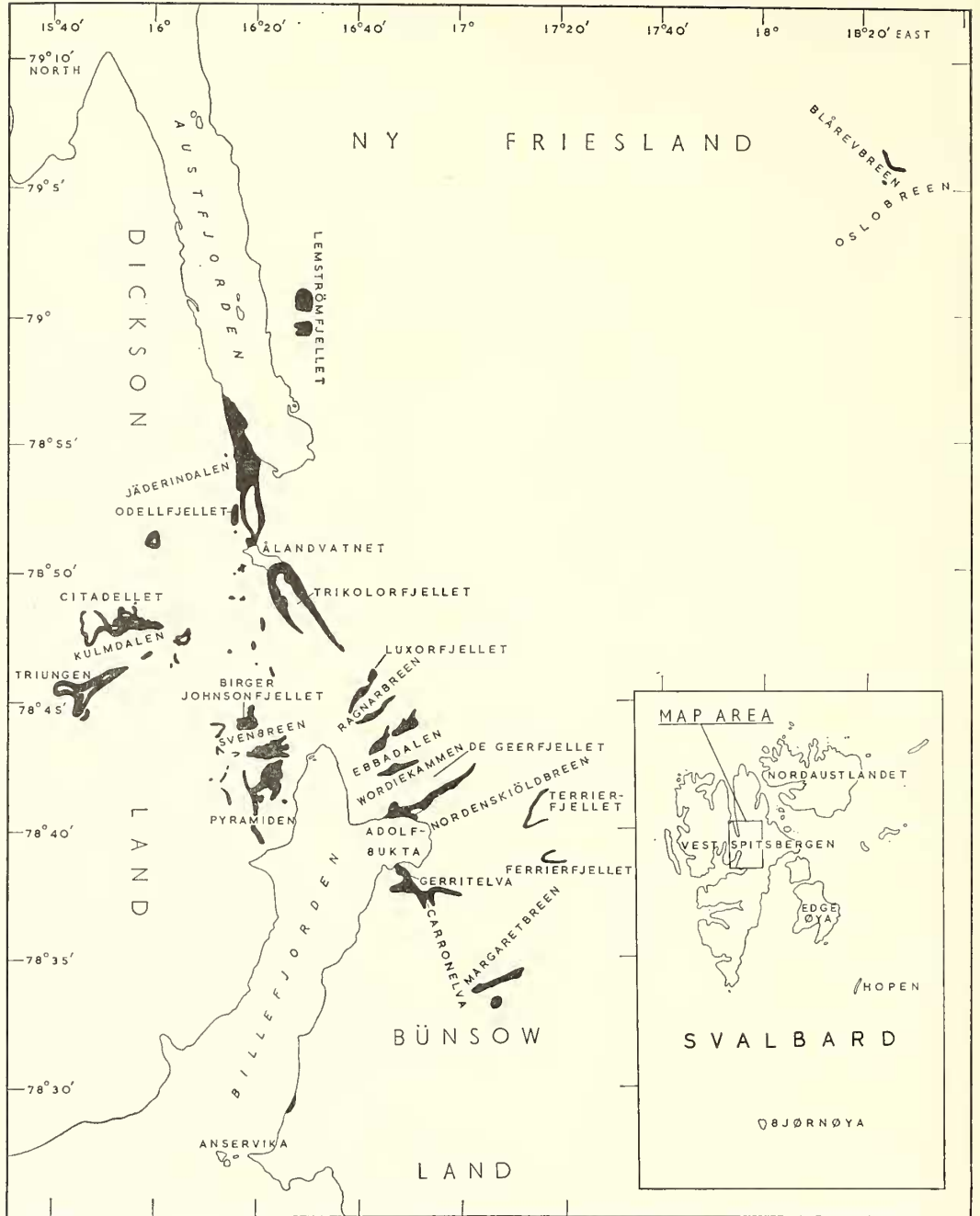
According to Gee *et al.* (1952, p. 312), late Palaeozoic deposition commenced over much of Svalbard in early Carboniferous times in a general submergence, following a period of extensive faulting, uplift, and erosion during the Upper Devonian. The irregular development of the Culm sediments strongly suggests their accumulation on a landscape of considerable relief. A graphic example is recorded by McWhae (1953, pp. 220-1) who describes a prominent buttress of pre-Downtonian (Hecla Hoek) basement over which Culm rocks are draped spectacularly in both the Ragnarbreen and

Ebbadalen areas. McWhae interprets this feature as a fault scrap (his hypothetical fault H) which must have been prominent in early Carboniferous time and had therefore resulted from (west block down) movement late in the Upper Devonian. This conjectural fault is traceable as a conspicuous basement step extending 'in a remarkably straight line from the east side of Wijdefjorden to the north-east corner of Adolfbukta at the foot of Nordenskiöldbreen' (McWhae 1953, p. 220).

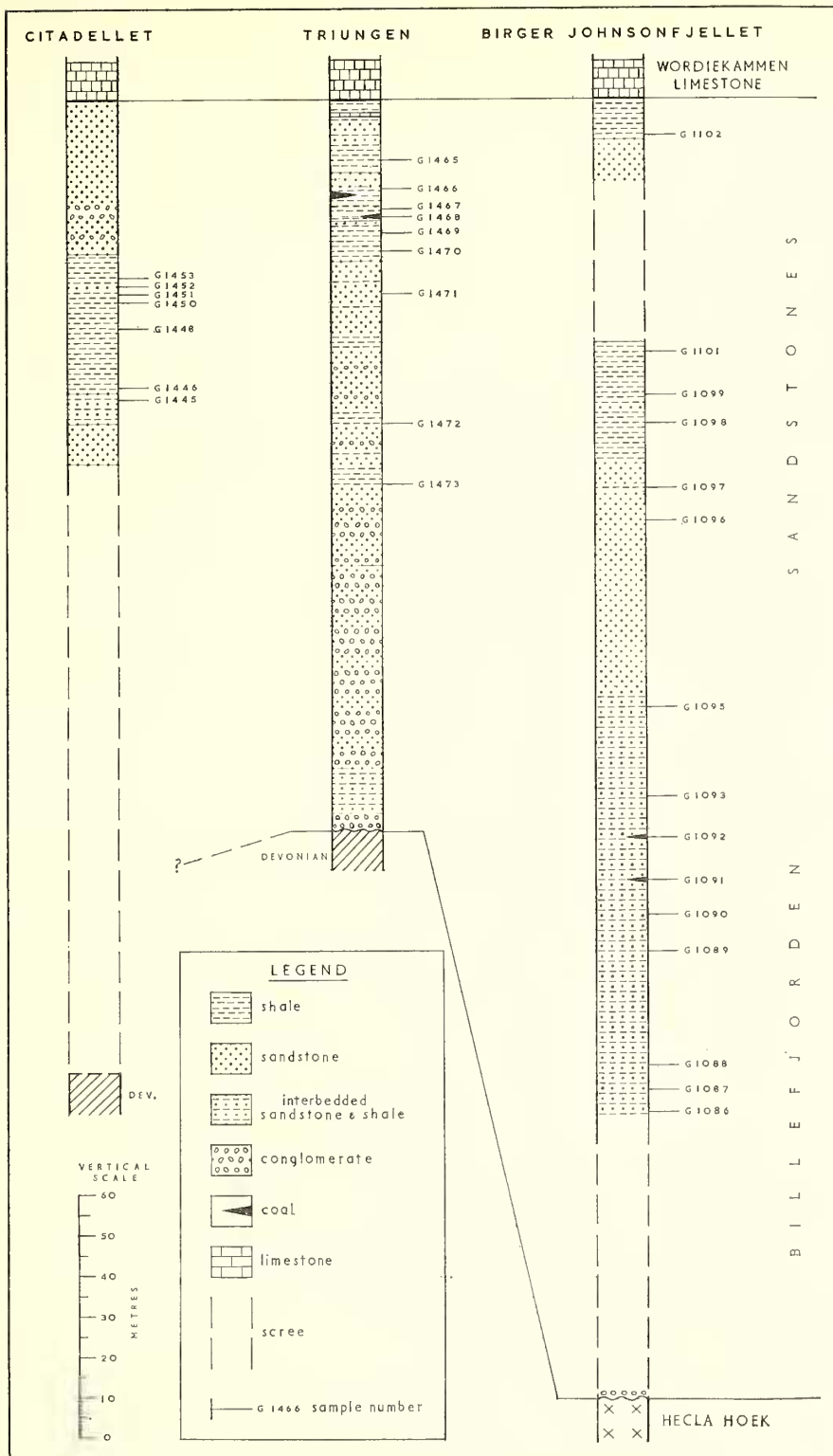
As shown in text-fig. 1 of Forbes *et al.* (1958), Lower Carboniferous deposits are exposed in Spitsbergen, principally in the central and extreme western parts of Vestspitsbergen; apparently isolated developments are also known in eastern Ny Friesland, Vestspitsbergen. Text-fig. 1, showing Culm outcrops in Central Vestspitsbergen, was compiled mainly from a comprehensive geological map prepared by Mr. P. F. Friend and based upon the field-work of Cambridge Spitsbergen Expeditions. The samples, constituting the basis of this study, were collected from the majority of localities indicated on text-fig. 1; for simplification of reference the only place-names included are those relevant to the outcrop positions. Contemporary exposures of the Billefjorden Sandstones represent remnants of a once more or less continuous development of strata in a depositional basin which, as noted by McWhae (1953, p. 212) and Forbes *et al.* (1958, p. 468), ran roughly north-south, approximately through the position of Wijdefjorden and Billefjorden. Relatively small exposures in eastern Ny Friesland, at Blårevbreen (text-fig. 1) and near Lomfjorden (see Forbes *et al.* 1958, text-fig. 1) may perhaps have been part of this continuous development in central Vestspitsbergen, which taken as a whole was 'possibly originally isolated from the deposits in western Spitsbergen' (Forbes *et al.* 1958, p. 468).

Three well-exposed and representative sections of the Billefjorden Sandstones, at Citadellet, Triungen, and Birger Johnsonfjellet, were collected for palynological purposes by Dr. D. J. Gobbett in 1959. Text-fig. 2, based upon Gobbett's detailed field notes, illustrates the succession at these localities together with the precise position of the samples which form an important basis for the present study. At Triungen and Birger Johnsonfjellet, the Billefjorden Sandstones rest unconformably upon the Devonian and Hecla Hoek rocks respectively; at Citadellet, the base of the Billefjorden Sandstones is scree-covered. The Lower Carboniferous sequence of all three localities is overlain disconformably by the Wordiekammen Limestones (Upper Carboniferous). Of other Culm samples examined from Citadellet and Triungen, B685 (studied by Hughes and Playford 1961) and B687 are from unspecified horizons at Citadellet; and G1461 was collected 23 metres stratigraphically below the base of the Wordiekammen Limestones in a section exposed about a quarter of a mile east of the Triungen section illustrated in text-fig. 2.

Many of the samples examined had been collected from various localities on the east side of Billefjorden, but as noted by Gee *et al.* (1952, p. 335) most of the Culm exposures in this area are largely covered by scree. On the south side of Ebbadalen, numerous samples (B604, B609, F531, F774, G332, G334, G366, G382) are from a thin coaly seam (and associated shales and siltstones) occurring 620 feet above the base of a Culm section measuring 840 feet in total thickness (McWhae 1953, fig. 6, stratigraphical column H); the microflora of B609 was recorded by Hughes and Playford (1961). Two samples (B706, W860) were collected from a similar succession exposed on the north flank of Ebbadalen; both are close to the local base of the Billefjorden Sandstones, which here



TEXT-FIG. 1. Map of part of Vestspitsbergen showing distribution of Lower Carboniferous, Culm, sediments (in heavy black); samples have been examined palynologically from the majority of localities indicated.



TEXT-FIG. 2. Stratigraphical columns of the Billefjorden Sandstones as exposed at Citadellet, Triungen, and Birger Johnsonfjellet, Vestspitsbergen (compiled from field notes of Dr. D. J. Gobbett).

conspicuously overlap the pre-Downtonian buttress mentioned previously. Farther north, 500 feet of Billefjorden Sandstones crop out on the north side of Ragnarbreen; sample R38 was collected approximately 90 feet above base. The formation is poorly exposed on De Geerfjellet, where a thickness of 'probably more than 700 feet' is reported by Gee *et al.* (1952, p. 335; pl. 2, stratigraphical column A); samples G636 and T269 are from a limited outcrop of interbedded shales and sandstones occurring in the bed of a small stream some distance west of column A cited above. Sample S59a was obtained from the north side of Wordiekammen, approximately 620 feet above the base of the Billefjorden Sandstones, which here attain a thickness of about 850 feet; the microflora of this sample was described by Hughes and Playford (1961). Sample W217 is from an outcrop on the north shore of Adolfbukta, about 400 yards west of Nordenskiöldbreen.

To the east of Adolfbukta, good exposures of the Culm are recorded by McWhae (unpublished data) at Terrierfjellet and Ferrierfjellet, with respective thicknesses of 325 feet and 175 feet. Several coal seams are included within a predominantly sandstone lithology, but unfortunately sampling was not undertaken.

Extending south-east from the south side of Adolfbukta, the Billefjorden Sandstones are exposed discontinuously in the vicinity of Gerritelva and Carronelva. According to Gee *et al.* (1952, p. 335; pl. 2, stratigraphical column E) the thickness at the latter locality is over 640 feet. None of the samples from Gerritelva (353, 390, 391) or from Carronelva (G1080) is from a specified horizon.

Two streams on the east and west sides of Margaretbreen, northern Bünsow Land, disclose respectively about 48 metres and 62 metres of Billefjorden Sandstones, consisting of interbedded sandstones and shales (D. J. Gobbett, field notes). Base is not exposed at either locality. Samples G1339 and G1344 are from the eastern and western sections respectively; G1339 is from a horizon about 30 metres stratigraphically below that represented by G1344.

A small coastal inlier of Billefjorden Sandstones occurs to the north of Anservika, western Bünsow Land. This was studied in detail by members of the 1949 Expedition. As stated by Gee *et al.* (1952, p. 336), correlation of these beds is uncertain owing to major dislocation of the area. Seven samples examined by the writer (R5, F20, D120, G1283, G1280, G1278, G1276) had all been collected from the 22-foot bed of 'carbonaceous sandstone with shaly partings and indeterminate leaf remains' occurring 32 feet above sea-level (Gee *et al.* 1952, p. 336). The total thickness of Culm exposed in the Anservika section is 316 feet, and its base lies somewhere below sea-level.

Coal-measure facies in the Culm are being mined by the Russians at Pyramiden, north-west Billefjorden, and as noted by Gee *et al.* (1952, p. 335) the strata are notably thinner here (about 80 metres) than on the east side of Billefjorden; no Pyramiden samples have been examined by the present writer. To the immediate north, at Birger Johnsonfjellet, the Culm increases in thickness to approximately 320 metres (see text-fig. 2). One sample examined (E363) is from Svenbreen, which is situated between Birger Johnsonfjellet and Pyramiden; it was obtained from just above the unconformable contact between the Billefjorden Sandstones and the Hecla Hoek.

Scattered Culm samples have come from exposures occurring between the south-western coast of Austfjorden and the north end of Ålandvatnet. From the latter locality, samples B616 and B619 are from a 50-foot section of Culm lying unconformably upon pre-Downtonian rocks (B. Moore, field notes). According to Moore, a faulted outlier

of Culm, resting unconformably upon pre-Downtonian rocks, occurs on the north summit ridge of Odellfjellet. Although not precisely located stratigraphically, samples B624 and B680 were collected respectively from near the top and bottom of this exposure which is some 170 metres thick; another sample (H267) collected earlier by Mr. W. B. Harland is probably from near the top of the exposure. Forbes *et al.* (1958, p. 468) quote a minimum of 500 metres as the comprehensive thickness of Billefjorden Sandstones in the Odellfjellet area. Numerous samples collected from around the south-west shore of Austfjorden failed to yield determinable microfloras.

Forbes *et al.* (1958, p. 468) mention the presence of at least 300 metres of Billefjorden Sandstones at Lemströmfjellet, immediately east of Austfjorden. Of samples examined from this locality, a recognizable microfloral assemblage was recovered from sample B443.

A remote exposure of Culm rocks occurs at Blårevbreen, a tributary of Oslobreen, in eastern Ny Friesland. Sample M365 was collected in 1952 by Mr. M. B. Bayly and samples Q55 and Q56 in 1959 by Mr. J. L. Fortescue from the poorly exposed Culm section, 30 metres thick, which rests unconformably upon Hecla Hoek rocks and is overlain (? disconformably) by massive, crag-forming, coral-bearing limestones, which are probably attributable to the Cyathophyllum Limestones.

Culm strata are developed along the western seaboard of Vestspitsbergen as a relatively narrow belt extending discontinuously southwards from Brøggerhalvøya, on the south side of Kongsfjorden, to the south-west side of Hornsund. Although no palynologically useful samples have been examined from this region by the writer, it is relevant to give some consideration here to this important development of the Spitsbergen Lower Carboniferous.

Whereas in Central Vestspitsbergen the Upper Palaeozoic rocks appear relatively undisturbed (apart from some rejuvenation in the Tertiary of mainly Devonian fractures), the western coast of Vestspitsbergen has been subjected to considerable earth-movements in the Tertiary causing strong folding, and in places overthrusting, of Palaeozoic and Mesozoic strata (Orvin 1940, pp. 42 *et seq.*). Thick sequences of Lower Carboniferous rocks are exposed at a number of localities, where they rest unconformably upon folded Hecla Hoek and are overlain, usually conformably, by ? Middle Carboniferous red beds. For the most part the Culm dips steeply to the east, locally becoming overturned (see Orvin 1940, pl. III).

An important section of Culm, 1,000 metres in thickness, on the north side of Bellsund, has yielded abundant plant material which was described by Nathorst (1914, 1920). Three clearly defined successive floras were distinguished (Nathorst 1920) as follows:

3. Diabasbucht flora with *Cardiopteridium nanum*, &c.
2. Hagerup Haus flora with *Sphenopteridium norbergii*, &c.
1. Camp Miller flora with *Adiantites bellidulus*, &c.

Forbes *et al.* (1958, p. 480) commented that the 'Hagerup Haus flora may be of approximately the same age as that of the shales at Pyramiden and Linnéelva'.

Other well-known exposures of Lower Carboniferous terrestrial beds occur at St. Jonsfjorden (325 metres in thickness, according to Dineley 1958), Trygghamna (700–800 m., Dineley 1958), Festningen (*c.* 700 m., Orvin 1940), Reinodden (*c.* 700 m.,

Orvin 1940), Ahlstrandodden (200 m., Orvin 1940), and at south-west Hornsund (930 m., Siedlecki 1960). Plant macrofossils have been reported from some localities; Nathorst (1914) lists collections from Örretelven (Festningen section), Ingeborgfjell (north Bellsund), Midterhukken (east Bellsund), and from Robertdalen (Reinodden section).

Macrofloras collected up to the present time do not permit more than a broad correlation between the Culm sequences of Central and of Western Vestspitsbergen (see Forbes *et al.* 1958, p. 480). On the other hand, palynological investigation of the latter may well provide a precise means of correlation with the Billefjorden Sandstones sequence with which the present study is primarily concerned. Through the courtesy of Professor O. H. Selling, of the Paleobotaniska Avdelningen, Naturhistoriska Riksmuseet, Stockholm, the present writer obtained fragments from plant-bearing Culm material collected in Western Vestspitsbergen by Swedish expeditions during the late nineteenth century and early twentieth century. These samples come from many of the localities listed by Nathorst (1914, 1920), viz. Diabasbukta, Hagerup Haus, Camp Miller, Ingeborgfjell, Örretelven, Midterhukken, and Robertdalen; unfortunately none yielded spores of any description. Perhaps it may be that the microfloras failed to survive the intensive Tertiary tectonism of Western Spitsbergen outlined above. In this connexion, the results should prove significant of a palynological investigation (Birkenmajer 1960, p. 30 footnote) being undertaken on samples from a Culm coal seam exposed at Sergejev-fjellet, south-west Hornsund (see Siedlecki 1960, p. 98).

Upper Palaeozoic rocks are exposed extensively on Bjørnøya (Bear Island), the southernmost island of Svalbard, situated some 120 nautical miles south of Spitsbergen. An admirable account of the geology of this island is contained in the 1928 publication of Horn and Orvin. In contrast to Spitsbergen, Bjørnøya is especially notable for the presence of a widespread terrestrial, plant-bearing deposit, the Ursa Sandstone, which was laid down apparently continuously during Upper Devonian and Lower Carboniferous times.

In 1902 Nathorst described his well-known Upper Devonian *Archaeopteris* flora from Austervåg (south of Engelskelva) and from five other localities, all on the east coast of Bjørnøya. Earlier, Heer (1871) had described a collection of plant macrofossils from a coastal section, the precise locality of which seems uncertain (see Forbes *et al.* 1958, p. 478) but is either to the immediate north or south of the mouth of Engelskelva. This collection included some Lower Carboniferous forms (e.g. *Lepidodendron veltheimi* Sternb., *Stigmaria ficoides* (Sternb.)) recognized as such by Heer, and in addition some probable Devonian floral elements. Confirmation of the existence of Lower Carboniferous strata on Bjørnøya came later from Antevs and Nathorst (1917), who reported the penetration of Culm strata, including a thin coal seam, in a borehole situated at the western outlet of Laksvatnet in the northern part of the island. The flora of these rocks included *Sphenopteris bifida* L. & H., *Adiantites cf. bellidulus* Heer, *Cardiopteridium cf. spetsbergense* Nath., and *Stigmaria ficoides* (Sternb.), all of which are well known from the Spitsbergen Culm.

At Nordkapp, on the north-east coast, Horn and Orvin (1928, pp. 82–83; fig. 50) recorded a coal seam occurring on the down-thrown (east) side of a fault in Culm sandstone which is considerably disturbed by faulting in the general area. All but one (P702) of numerous palynological samples collected by the writer from this section failed to

yield a determinable microflora. Approximately 100 yards east of, and about 50 feet stratigraphically below, this coal seam, abundant plant fossils were observed in a 10-foot band of carbonaceous shaly siltstone and fine-grained sandstone. Fossils collected from this horizon comprise:

<i>Calamites</i> sp.	* <i>Knorria</i> '
* <i>Lepidodendron spetsbergense</i> Nathorst	<i>Stigmara ficoides</i> (Sternberg) Brongniart
<i>Lepidodendron ?heeri</i> Nathorst	<i>Cardiopteridium ?spetsbergense</i> Nathorst (pinnules)
<i>Lepidodendron</i> sp.	* <i>Carpolithus</i> sp.

In addition, one sample (P725), which bears macrofossils marked * above, contains an identifiable microflora.

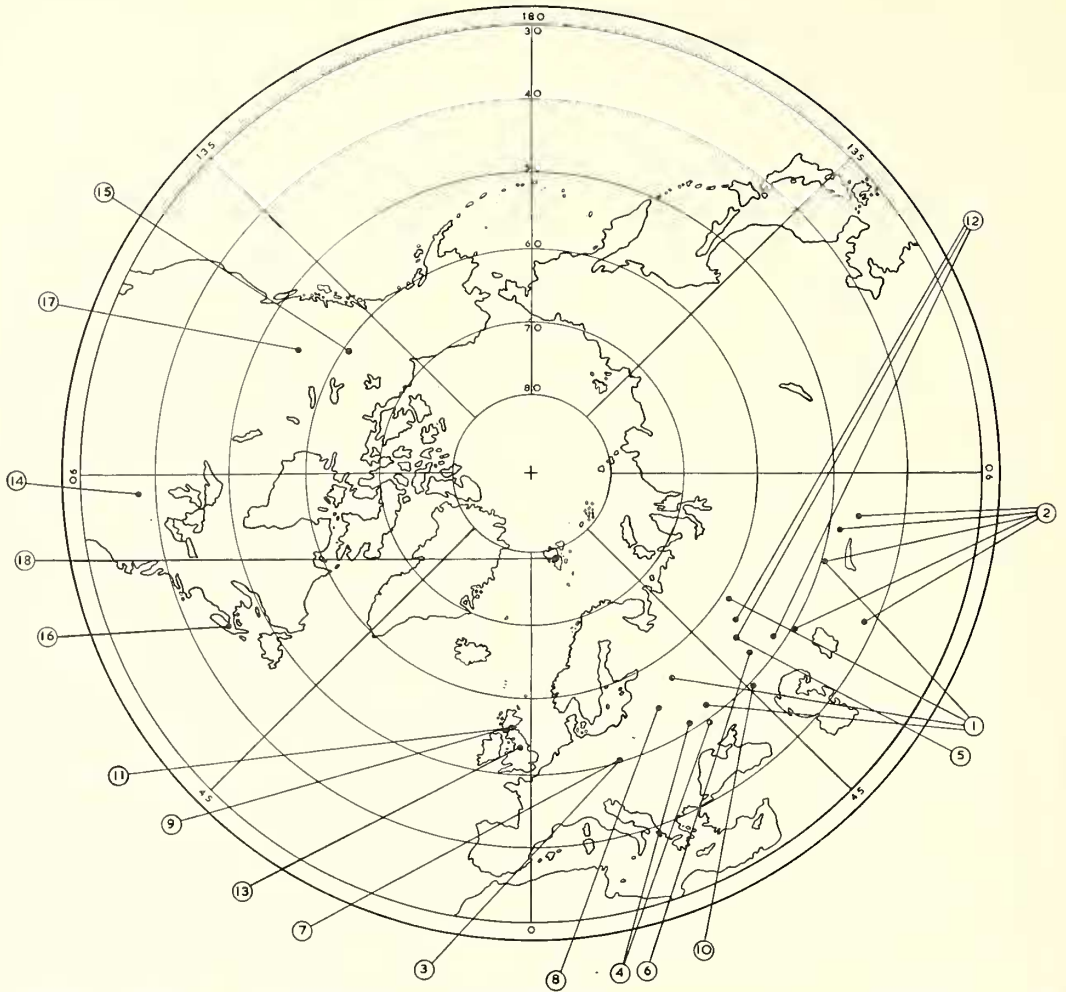
Numerous other samples collected from the majority of the Culm exposures on Bjørnøya are apparently devoid of spores; this may possibly be due to adverse weathering effects.

PREVIOUS INVESTIGATIONS OF LOWER CARBONIFEROUS MICROFLORAS

Until comparatively recently, palynological work on Carboniferous strata has been concerned mainly with the upper part of the System, due to the economic importance of coal seams contained therein, particularly in Great Britain and the United States. Thus microfloras, especially in coals, of Westphalian age are now known in considerable detail, and their useful application to problems of coal seam correlation has been demonstrated conclusively. With the widespread recognition of the unique value of fossil spores in the elucidation of general stratigraphical problems, an increasing amount of attention has been paid over the past few years to the microfloral content of other portions of the geological column. In the case of the Lower Carboniferous, a review of the steady stream of more recent palynological publications provides ample testimony that, in the Northern Hemisphere at least, precise correlation by palynological methods is possible between widely separated non-marine sequences of this age. A limiting factor is the all-important systematic aspect of palynology: it can scarcely be said that equilibrium has been reached in the taxonomy of fossil spores, but this is a not unexpected consequence of a relatively new and rapidly evolving science.

In the following paragraphs a brief review of published work on older Carboniferous microspore assemblages is presented. As far as possible, the fullest details are given concerning the stratigraphical position of such assemblages. This is deemed an essential preliminary to the assessment of the local and regional stratigraphical significance of a number of Spitsbergen spore species which are either identical with or closely related to certain elements of these previously recorded microfloras. Where it is known, detailed reference to extra-Spitsbergen occurrences of individual species is incorporated within the Systematic Section.

From text-fig. 3 it is apparent that Lower Carboniferous small-spore assemblages have been investigated from numerous, often widely separated localities. The stratigraphical interval covered by each individual author is recorded in text-fig. 4, and the geographical position of their described assemblages is shown on text-fig. 3. It is a convenient if perhaps precursory step at this stage to include the Spitsbergen sequence in text-fig. 4; microfloral evidence as to its placement will be adduced in a subsequent section of this paper.

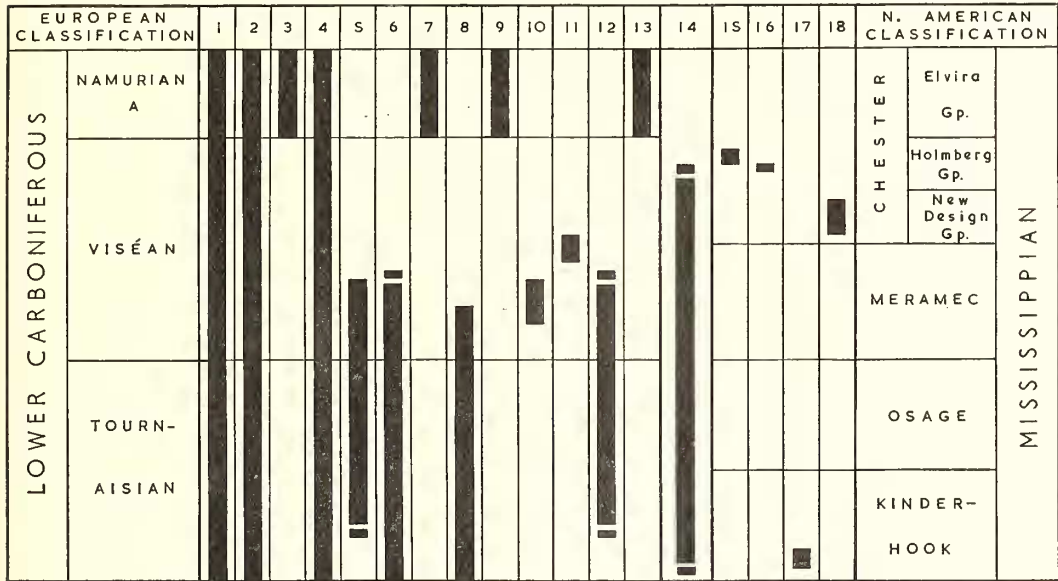


TEXT-FIG. 3. Localities from which Lower Carboniferous microspore assemblages have been described (or recorded) in the Northern Hemisphere. Index to authors—1, Luber and Waltz 1938, 1941; 2, Luber 1955; 3, Horst 1955; 4, Ishchenko 1956, 1958; 5, Bludorov and Tuzova 1956; 6, Byvsheva 1957; 7, Dybová and Jachowicz 1957; 8, Kedo 1957, 1958, 1959; 9, Butterworth and Williams 1958; 10, Loginova 1959; 11, Love 1960; 12, Byvsheva 1960; 13, Neves 1961; 14, Hoffmeister, Staplin, and Malloy 1955; 15, Hacquebard and Barsz 1957; 16, Hacquebard 1957; 17, Staplin 1960; 18, Hughes and Playford 1961, and present study.

The substantial, excellently illustrated publication of Reinsch (1884) is generally acclaimed as the most outstanding of earlier contributions to our knowledge of fossil microfloras. Most of the spores (both micro- and megaspores) had been recovered from coals of a number of localities, mainly in central Russia and also in Saxony. Unfortunately, Reinsch did not specify the age of the strata more precisely than 'Carboniferous', although it is evident from his illustrations that a considerable number of Lower Carboniferous types were represented. He believed that the organisms he found in the

Russian and Saxonian coals were of algal origin. Due to uncertainty regarding stratigraphical horizons and some localities, the work of Reinsch is not included on either text-figs. 3 or 4, but this is not intended to minimize or detract in any way from what must still be regarded as an essential reference for the worker on Lower Carboniferous microfloras.

In 1931 work was initiated by Russian palynologists on the spore content of Upper



TEXT-FIG. 4. Showing age and relative stratigraphical position of Lower Carboniferous microspore assemblages recorded from the Northern Hemisphere. Correlation of the European and North American subdivisions is based upon Weller *et al.* (1948). Broken limits of columns represent uncertainty regarding precise age limits. Index to authors—1, Luber and Waltz 1938, 1941; 2, Luber 1955; 3, Horst 1955; 4, Ishchenko 1956, 1958; 5, Bludorov and Tuzova 1956; 6, Byvsheva 1957; 7, Dybová and Jachowicz 1957; 8, Kedo 1957, 1958, 1959; 9, Butterworth and Williams 1958; 10, Loginova 1959; 11, Love 1960; 12, Byvsheva 1960; 13, Neves 1961; 14, Hughes and Playford 1961, and present study; 15, Hoffmeister, Staplin, and Malloy 1955; 16, Hacquebard and Barss 1957; 17, Hacquebard 1957; 18, Staplin 1960.

Palaeozoic strata, principally Carboniferous coals, of the U.S.S.R. This culminated in the important publication of Luber and Waltz (1938), which contains a systematic and stratigraphical account of spore complexes occurring in Russian coals of Tournaisian-Viséan and of Middle and Upper Carboniferous age. The bulk of the investigation was concerned with the microfloral content of Tournaisian, in part Viséan, coals of the Moscow Basin, Kizel district, Borovichi district, Selizharovo district, and Voronezh region; and of exclusively Viséan coals of the Karaganda Basin. The first five localities (all in European Russia) were characterized by a fairly uniform Lower Carboniferous microfloral suite dominated by cingulate spores. In contrast, more or less contemporary microfloras of the Karaganda Basin (Asiatic Russia) comprised mainly azonate forms having spinose-tuberculate sculpture. On this basis, Luber and Waltz (1938, p. 42) deduced 'the existence of a peculiar provincial flora in the Karaganda region, differing

from the European and characterized by strict endemism'. These authors also noted a marked difference between the specific composition of their Lower Carboniferous microflora as a whole, and that of the Middle-Upper Carboniferous assemblages.

A subsequent major publication (Luber and Waltz 1941) included the description of 262 species of microspores and pollen grains recovered from Russian strata (predominantly coals) ranging in age from Devonian to Permian. Forms characteristic of each geological subdivision were listed. Most of the Lower Carboniferous species instituted in the earlier paper (Luber and Waltz 1938) were refigured, but in addition many new species of the same age were described and illustrated. Both publications have proved invaluable references in connexion with the present study and have revealed a striking similarity between the Spitsbergen Culm microfloras recorded herein, and those of the Russian Lower Carboniferous.

Luber (1955) made a further study of Middle and Upper Palaeozoic spores of Kazakhstan (including the Karaganda Basin). A number of supra-specific taxa were instituted (e.g. *Filictriletes*, *Calamotriletes*, *Asterocalamotriletes*, *Lycopodizonotriletes*, &c.) all having implied botanical affinities. Her Lower Carboniferous forms contrast strongly with those of the European part of Russia, and indeed bear little resemblance to the Spitsbergen spores.

Two recent substantial publications of Ishchenko (1956, 1958) contain the results of an intensive palynological investigation of the Lower Carboniferous sediments of the vast Donetz Basin. The first is concerned with the western extension of the Basin, and the 1958 paper deals with the Dnieper-Donetz Basin. Many new spore species are described and stratigraphical ranges within the Lower Carboniferous of individual forms are documented in considerable detail, especially in the 1956 paper. The 1958 range charts are less precise within the confines of the Lower Carboniferous but extend downwards into the Famennian and upwards as high as the Moscovian. Numerous species were recorded as possessing limited vertical distribution. On the basis of these, and that of relative abundance studies, Ishchenko was able to delimit three distinct microfloral suites, characteristic respectively of the Tournaisian, Viséan, and Namurian stages. The successful application of these to correlative problems of boreholes within the basin was also reported by Ishchenko (1958). It will be shown subsequently that the Spitsbergen microfloras bear a close similarity in many respects with those described from the Russian Lower Carboniferous by Ishchenko, as also by Luber and Waltz. In particular, Ishchenko's precisely recorded vertical distribution studies find direct application in the external correlation of the Spitsbergen Lower Carboniferous succession.

A number of short Russian papers—Bludorov and Tuzova 1956; Byvsheva 1957, 1960; Kedo 1957, 1958, 1959; Loginova 1959—record the occurrence of many of Luber and Waltz's (1938, 1941) species in horizons of the Tournaisian and Viséan, as developed in various parts of the U.S.S.R. Bludorov and Tuzova (1956) were concerned with the Lower Carboniferous Coal Measures of Tartary; Byvsheva (1957) with terrestrial Lower Carboniferous from the Melekes and Busuluk deep wells; Kedo (1957, 1958, 1959) with the Lower Carboniferous of White Russia; Loginova (1959) with the Yasnopolyansky substage (Lower Viséan) of the Saratov-Stalingrad Volga area; and Byvsheva (1960) with the terrestrial Lower Carboniferous of the Volga-Ural region. None of these papers contains systematic spore descriptions. Their value is diminished

somewhat by their listed occurrence of a considerable number of species which are attributed to Naumova (and often appear to have stratigraphical significance) but whose description and illustration remain obscure.

Supposed angiosperm-type pollen grains have been reported by Naumova (1950) from the Lower Carboniferous of the Moscow Basin, and subsequently by Teteriuk (1956, 1958) from approximately contemporary strata of the Donetz Basin. Such forms (*Tetraporina*) are of rare occurrence in the Spitsbergen Culm and will be discussed in the Systematic Section below.

Apart from the Russian work mentioned above, palynological investigation of the European older Carboniferous has been concerned mostly with sediments of Namurian age. Indeed, very little is known as yet of the spore content of Tournaisian and Viséan strata of western Europe.

Microfloras of the Upper Silesian Coal Measures have been described by Horst (1955) and by Dybová and Jachowicz (1957). The age of these coal measures ranges from Lower Namurian A to Westphalian D. Horst's investigation was mainly on the Namurian A strata, whilst Dybová and Jachowicz made a comprehensive study of 156 coal seams occurring throughout the sequence.

In 1958 Butterworth and Williams presented a concise account of the spore assemblages recovered from coals of the Limestone Coal Group and the Upper Limestone Group (Namurian A) of the Scottish Lower Carboniferous. This amplified to some extent the earlier work of Knox (1948) on spores from the Limestone Coal Group. Many of the spores described by Butterworth and Williams compare closely with those identified from Upper Silesia by Horst (1955) and by Dybová and Jachowicz (1957).

A sequence of microspore zones has been proposed recently (Butterworth and Millott 1960) in the coalfields of Britain, ranging in age from Upper Viséan to at least Westphalian D. Each zone is defined by the presence of an index microspore species. Their Microspore Distribution Chart shows the stratigraphical extent of these respective zones, and incorporates also the ranges of microspore genera as evidenced by various coal microfloras.

Love (1960) recorded spore assemblages occurring in certain horizons of the Lower Oil-shale Group (Viséan) of Scotland. From his Table 2, a downward extension is evident of many of the Scottish Namurian species described by Butterworth and Williams (1958). Love considered that his assemblages may be equated to the *Campotriletes verrucosus* Zone of Butterworth and Millott (1960), which had been delineated in coals of the Scremerston Coal Group and Lower Limestone Group (Viséan) of Northumberland.

Neves (1961) has described selected spores from Namurian coals and shales occurring in the Southern Pennines region of central England. This work is of especial stratigraphical significance in that the strata investigated may be referred directly to the established Namurian sequence of goniatite stages.

Hoffmeister, Staplin, and Malloy (1955) contributed a major work on Upper Mississippian microfloras from Illinois and Kentucky, U.S.A. Their described assemblages are from coals and shales of the Hardinsburg formation, which is equivalent in age to part of the Homburg division of the Chester series. These authors emphasized the importance of examining spore assemblages from clastic sediments as well as from coal seams, in order to obtain a more comprehensive, less environmentally restricted picture of the contemporary flora.

Another North American microflora of Upper Mississippian age is recorded by Hacquebard and Barss (1957). This microflora is from a thin coal seam occurring within, and 650 feet above the base of, the Mattson formation of the South Nahanni River area, Northwest Territories, Canada. According to Patton (1958, p. 324 and fig. 6), who collected the single sample, its age is equivalent to that of the mid-Meramec series of the standard North American Mississippian. More recently, however, Harker (1961, p. 8) states that the Mattson formation must post-date the Meramec because it conformably overlies beds containing a convincingly lower Chester marine fauna. Thus, the coal concerned is of middle or perhaps upper Chester age. Many of the spores described by Hacquebard and Barss are represented in the Russian Lower Carboniferous, and also, as shown below, in upper horizons of the Spitsbergen Culm.

Hacquebard (1957) described small-spore floras present in two coals from the Horton group (Mississippian) of Nova Scotia, Canada. The age of these coals is not known precisely, but on macrofloral and general stratigraphical evidence is certainly low in the Mississippian (Hacquebard 1957, p. 302). Certain aspects of the Horton microflora are discernible in assemblages from the lower horizons of the Billefjorden Sandstones; this resemblance will be amplified subsequently.

An important recent contribution is that of Staplin (1960), who described an abundant microflora from the Golata formation (Upper Mississippian) of Alberta, Canada. Numerous species described by Staplin are recorded herein from the upper part of the Spitsbergen Lower Carboniferous. According to Staplin's text-fig. 1, the Golata formation is equivalent in age to the lower part of the Chester series, and is thus probably somewhat older than the coal investigated by Hacquebard and Barss (1957).

The first published record of Lower Carboniferous spores in the Southern Hemisphere is contained in a recent paper by Balme (1960), who in addition investigated sediments of Upper Carboniferous age. The microfloras were obtained from the Laurel Beds (Lower Carboniferous) and from the Anderson Formation (Upper Carboniferous) of the Fitzroy Basin, Western Australia. Spore identifications were almost entirely on a generic level, although specific morphological characters were listed briefly. Balme noted some similarities between his Lower Carboniferous assemblages and those of the United States and the U.S.S.R.

With regard to dispersed-spore studies of the Spitsbergen Lower Carboniferous the only publication prior to Hughes and Playford (1961) is that of Lubert (1935), who figured but did not describe or name several spores from the Culm of Pyramiden. She noted a general resemblance of the microflora with that of the Russian Lower Carboniferous; this was reiterated by Lubert and Waltz (1938, p. 42) and is confirmed abundantly in the present investigation.

Of particular interest is a recent reinvestigation (Bharadwaj 1959) of the fructification *Porostrobos zeileri* Nathorst, which had been collected in 1882 by Nathorst from Pyramiden, Spitsbergen. From this cone, Bharadwaj obtained spores conformable with the dispersed-spore genus *Densosporites*. It will be shown subsequently that these spores, as described and illustrated by Bharadwaj, closely resemble a type which occurs in many of the samples examined by the present writer.

With reference to text-fig. 4, it is necessary to give some consideration here to the correlation of the North American Mississippian succession with the standard Carboniferous stages of western Europe. The combined equivalence of the Kinderhook

series and the overlying Osage series with the Tournaisian appears to be well established on the basis of the diagnostic *Spirifer tornacensis* fauna (Moore 1937, p. 660). However, as noted by Weller *et al.* (1948, p. 108), precise delineation of the Viséan boundaries in North America presents some difficulty owing to the fact that certain ammonoid genera (notably *Beyrichoceras*, *Eumorphoceras*, and *Goniatites*), which are stage indices in western Europe, appear to have different ranges on the other side of the Atlantic. Lithostrotionid coral faunas testify to the Viséan age of the Meramec series, and the general correspondence of the Namurian with the upper Chester series seems well established (Weller *et al.* 1948; Elias 1960). However, the position of the Viséan–Namurian boundary in the North American succession has been subject to some conjecture owing to the much earlier North American occurrence (in lower Meramec beds) of *Eumorphoceras*, the European introduction of which marks the beginning of the Namurian. Weller *et al.* (1948, p. 108) summed up the situation as follows: ‘the Viséan–Namurian boundary may correspond with the division between the Chesterian and the Meramecian, or it may fall within the Chesterian’. The latter correlation, as given on their chart (and on text-fig. 4, herein), was considered the more likely in view of the mid-Chester occurrence (in Arkansas and Oklahoma) of *Goniatites* which is unknown in European strata of post-Viséan age. More recent goniatite and conodont evidence also supports the placement of the Viséan–Namurian boundary within the Chester, approximately at the base of the Elvira group (Elias 1960, p. 152; Higgins 1961, p. 221). On the other hand, from Russia Stepanov (1959, p. 64) equates the base of the Namurian with that of the Chester series, but does not cite any palaeontological or other evidence for this correlation.

As outlined above, microfloras described by various authors from the Russian Lower Carboniferous have much in common with those of the present study. The strata from which the Russian microfloras have been documented are almost always recorded as being dated in varying degrees of precision with reference to the western European stages. A critical examination of two recent Russian stratigraphical publications, Librovitch (1958) and Aisenverg *et al.* (1960), indicates that such dating is, in fact, based reliably upon extensive studies of marine faunas, especially those of the Russian Platform and the Donetz Basin. Thus although microfloras have not been recorded from the type areas of the Lower Carboniferous stages, these latter divisions may be delineable reliably, if indirectly, in the Spitsbergen succession, through the correlative medium of the Russian Lower Carboniferous.

PREPARATION AND EXAMINATION OF SAMPLES

The samples studied comprise a fairly wide variety of lithological types, ranging from coals to medium-grained sandstones, all of apparently continental origin. It is difficult to generalize with regard to the most productive rock type. Perhaps the most generally reliable was the carbonaceous shale or siltstone, but then this lithology had been collected abundantly and preferentially from the Spitsbergen Culm with palynological work in mind. A number of fine-grained sandstones yielded exceedingly diverse and well-preserved spore assemblages. With such a variety of lithological types at hand, it proved essential, as a prerequisite in planning subsequent maceration procedure, to examine each specimen individually and to record macroscopic observations. Broadly

speaking, the samples were separable in the first instance into two categories—highly carbonaceous sediments (mainly coals) and clastics with less carbonaceous material.

Initially, mechanical disintegration involved crushing of the sample—*c.* 5 grammes of clastic sediment or 2 grammes of coal—to a size of about 1 millimetre. To minimize risk of contamination crushing of each sample was done on several layers of clean newspaper placed on an iron block. The hammer was cleaned carefully before and after the sample had been ground.

Coals were macerated by means of Schulze solution (concentrated nitric acid and potassium chlorate). The time for adequate maceration of individual samples was variable, ranging from 3 to 15 hours. An alternative procedure using fuming nitric acid, for a maximum of 4 hours, yielded comparable spore concentrations, but in many cases individual species appeared overmacerated. Following maceration and washing, the residue was treated with 1 per cent. ammonium hydroxide; in some instances, additional treatment with as strong as 10 per cent. ammonium hydroxide was necessary in order to solubilize excessive amounts of oxidized material. This step was found by experience to be one of the more critical phases of the process; indiscriminate use of strong alkali following oxidation proved highly destructive in many preparations. If the residue contained a conspicuous amount of mineral matter it was allowed to stand overnight in cold, 50–60 per cent. hydrofluoric acid.

Clastic sediment samples were initially placed in nickel crucibles, to which 50–60 per cent. hydrofluoric acid was added and boiled for 30–45 minutes. The residue was washed thoroughly, and in some preparations a 5-minute treatment with warm, 20 per cent. hydrochloric acid was necessary to dissolve fluorides resulting from the HF treatment. Oxidation of the humic material was then carried out with Schulze solution. Maceration time was much less than for coals; it ranged from 10 minutes to 4 hours. Subsequent alkali treatment was not invariably required for satisfactory spore concentrations, but where necessary it was undertaken with caution as in coals above.

In the preparation of many coals and clastics, a 15–30 seconds' treatment with an ultrasonic disintegrator (1:1 end ratio steel probe vibrating at 20 kilocycles per second) proved highly effective in disaggregating clumps consisting of spores and other organic or mineralogical matter. In the case of coals, it was undertaken following the maceration step, and with clastics, immediately after the HF processing; disaggregation was accomplished in an aqueous medium containing a few drops of non-ionic detergent. Great care was necessary as excessive ultrasonic treatment was shown to cause considerable, often preferential, damage to the spores.

Fifty per cent. glycerine containing a few drops of phenol was added to the ultimate, thoroughly washed residues, which were then transferred for storage to small plastic-stoppered glass tubes. Adequate natural colour of the spores made staining unnecessary. Glycerine jelly was used for mounting of the residues. At least three slides were made from each residue, dependent upon its richness. In addition, over 200 spores were mounted singly, following the method described by Balme (1957, p. 13). Cover slips of all slides were sealed with gold size at least three days after mounting.

Initially, all slide preparations were scanned thoroughly at a magnification of $\times 120$, and preliminary determinations of, and morphological observations on, species present were recorded from high power ($\times 450$) magnification. The first samples examined systematically in this manner were those from the well-documented successions at

Birger Johnsonfjellet, Triungen, and Citadellet. These gave an overall picture of the sequence of microfloras represented in the Spitsbergen Lower Carboniferous. Subsequent counting (250 specimens from each preparation) under high power enabled a quantitative estimation of the microspore species present in most of the samples from the three successions; a few of the samples, however, yielded insufficiently concentrated and poorly preserved microfloras such that meaningful counting was precluded. Preparations of numerous samples from other localities were then examined, and comparisons could be drawn between their microfloral content and that of individual samples from the three reference successions mentioned above, with a view to local correlation within Spitsbergen. Detailed systematic descriptions set out below were undertaken only after all the productive samples had been examined. The oil-immersion objective was used extensively in the elucidation of spore morphology.

SYSTEMATIC DESCRIPTIONS OF DISPERSED SPORES

Preliminary remarks. The morphographical system initiated by Potonié and Kremp (1954), and subsequently amplified by these authors (Potonié and Kremp 1955, 1956a; Potonié 1956, 1958, 1960) is followed throughout. From the point of view of the stratigraphical palynologist, this entirely artificial scheme is undoubtedly the most satisfactory presented to date, as it represents a comprehensive, readily applied method for the classification of dispersed spores, many of which have uncertain botanical affinities, but often considerable stratigraphical significance. Knox (1950, pp. 308–9) stated the case for artificial classification as follows: ‘A natural classification of fossil spores is at present practically impossible, since few of the spores so far described have been found in organic connection with the parent plant. It is thus necessary to formulate an artificial system using the various features which have been found to be of diagnostic value.’ Within the artificial framework, the documented botanical affinities of the morphographical spore taxa should be indicated wherever known. These can be based reliably only upon studies of the spore content of fossil fructifications, whose fossil record can unfortunately never approach that of the wealth of dispersed spores available. Certainly, it seems erroneous to endeavour to relate fossil spores, particularly of Palaeozoic age, to modern plant groups on the basis of spore morphology alone. In the systematic section below, known botanical affinities are given of the various microspore genera represented in the Spitsbergen material.

The term microspore is here used in the broad sense of dispersed fossil ‘small spores’ of diameter less than $200\ \mu$, corresponding thus to ‘miospore’ which was introduced by Guennel (1952, p. 10) to embrace ‘all fossil spores and spore-like bodies smaller than 0.20 mm., including homospores, true microspores, small megaspores, pollen grains, and pre-pollen’.

In the systematic section below, the writer has attempted to use only those descriptive terms which appear to find widespread acceptance among palynologists. Sculptural terms employed are mainly those defined by Harris (1955, pp. 18–21); as far as possible their use is amplified by detailed measurements of the size and spacing of individual sculptural elements in an attempt to obviate differing connotations which exist in the case of many of these terms.

Following Potonié and Kremp (1955), the terms intexine and exoexine are used to denote respectively the inner and outer layers of the spore wall (exine).

Nomenclature for equatorial structures (cingulum, auriculae, zona, corona, limbus) is applied in the defined sense of Potonié and Kremp (1955). In addition, the term patina of Butterworth and Williams (1958) is used. Mention will also be made (see the genus *Monilospora*) of the 'capsula-patella' terminology of Staplin (1960), the use of which appears superfluous.

The term laesurae is here applied to the proximal polar dihiscence apertures (see Erdtman 1952, p. 12) and is thus synonymous with 'commissure(s)' of Harris (1955, p. 25) and Couper (1958, p. 102) and with 'Y-mark' of Potonié and Kremp (1955, p. 10). In the present context 'lips' denotes a conspicuous modification, usually a marked increase in thickness, of the exoexine immediately adjacent to the laesurae (see Harris 1955, p. 13).

The amb is defined by Erdtman (1952, p. 459) as the outline of a spore or pollen grain viewed from the direction of the polar axis.

Unless otherwise stated, the measurements given in the descriptions which follow were obtained from specimens preserved in full polar view. In the case of triangular forms, the equatorial diameter was taken as the maximum median length, and for quadrangular forms, the maximum diagonal length was measured.

All microspore species are illustrated by means of photographs from unretouched negatives; in addition, some camera-lucida drawings are given. New species have been instituted only where at least fifteen adequately preserved specimens have been available. Particular care has been given to describing these and all other forms from the largest possible number of samples, especially in order to appreciate the aspect of any particular species in varying states of preservation. Definite assignment to previously described species has been made only where reasonably conclusive identity could be demonstrated by reference to original descriptions and illustrations of apparently well-preserved types. Conspecificity is often difficult to establish, particularly in the case of Russian forms, which are often inadequately described and illustrated only by drawings. Thus several new species are qualified by statements to the effect that they may be identical to certain previously instituted types.

A number of ostensibly discrete, previously described species are shown to be linked by a continuous and not extreme morphographical variation as observed consistently in the preparations of many samples. For example, *Murospora aurita* (Waltz) comb. nov., emend., demonstratively includes several forms originally instituted as separate species, which are considered here merely as infraspecific morphographical variations.

Many genera of Palaeozoic *sporae dispersae* are poorly circumscribed, mutually overlapping, and of doubtful validity. Thus the generic assignment of some of the species described herein may well prove debatable. However, controversy regarding generic assignment should not obscure the fundamental importance of concise description and illustration at specific level, an undoubted prerequisite for meaningful generic institutions as for the useful application of palynology to stratigraphical correlation.

All type and other figured specimens of the present study are referred to by the preparation/slide number, followed by the 'east-west' and 'north-south' mechanical stage readings, and then the Sedgwick Museum Specimen number (prefixed 'L'). The stage readings are from Leitz Dialux microscope no. 1 (serial no. 469843) in the Sedgwick Museum, Cambridge, where the material is deposited (specimen registration numbers L.939-L.1258). The registered numbers (L.880-L.938) have also been given to all type and other figured specimens of Hughes and Playford (1961).

Anteturma SPORONITES (R. Potonié) Ibrahim 1933

Genus CHAETOSPHAERITES Felix 1894

Type species (here designated). *C. bilychnis* Felix 1894, pp. 272–3; pl. 19, fig. 4.

Affinity. The type species, which is of Eocene age, was allied by Felix (1894, p. 273) to spores borne by several species of the recent *Chaetosphaeria*, a member of the fungal family Ascomycetaceae.

Chaetosphaerites pollenisimilis (Horst) Butterworth and Williams 1958

Plate 78, figs. 1, 2

1955 *Sporonites pollenisimilis* Horst, pp. 150–1; pl. 24, figs. 84–87.

1957 *Sporonites cylindricus* (Horst) Dybová and Jachowicz, pp. 56–57; pl. 1, figs. 1–4.

1958 *Chaetosphaerites pollenisimilis* (Horst) Butterworth and Williams, p. 359; pl. 1, figs. 1–3.

Description. In addition to the usual bicellular forms, occasional specimens possessing one or three translucent ‘heads’ were encountered. Measurement of thirty-five specimens gave a size range of 21–52 μ (mean 36 μ).

Previous records. *Chaetosphaerites pollenisimilis* (Horst) has been recorded previously from European strata of Namurian age (Horst 1955; Dybová and Jachowicz 1957; Butterworth and Williams 1958), from the Golata formation (Upper Mississippian) of Canada (Staplin 1960), and from one sample (S59a) of the Spitsbergen Lower Carboniferous (Hughes and Playford 1961). Butterworth and Millott (1960) indicate Viséan–Namurian distribution in British coals.

Anteturma SPORITES H. Potonié 1893

Turma TRILETES (Reinsch) Potonié and Kremp 1954

Subturma AZONOTRILETES Lubert 1935

Infraturma LAEVIGATI (Bennie and Kidston) R. Potonié 1956

Genus LEIOTRILETES (Naumova) Potonié and Kremp 1954

Type species. *L. sphaerotriangulus* (Loose) Potonié and Kremp 1954.

Discussion. The validity of this genus, as emended in 1954 by Potonié and Kremp and generally applied exclusively within the confines of Palaeozoic palynology, has been questioned by Staplin (1960, p. 14), who assigned simple, smooth, triangular, trilete spores of Mississippian age to the genus *Deltoidospora* Miner 1935, which is often ‘reserved’ for post-Palaeozoic spores. Contrary also to usual practice, Nilsson (1958, pp. 30–33) included within *Leiotriletes* similar spores occurring in Swedish Liassic sediments.

The present writer is in agreement with Staplin’s (1960) statement—‘the argument that there is a separation in time between Miner’s species and species referred to *Leiotriletes* has little validity where form genera are concerned’. However, the question seems far from resolved, particularly in view of Potonié’s (1960, pp. 26–27) lengthy discussion, and accordingly the Spitsbergen spores concerned are assigned herein to *Leiotriletes*.

The problem is not, of course, restricted to *Leiotriletes*, but concerns equally the relationship between such comparatively characterless form-genera as *Punctatisporites* and *Calamospora*, and their Mesozoic equivalents.

Affinity. Representatives of *Leiotriletes* have been reported recently by W. and R. Remy (1957) from

the fern fructifications *Oligocarpia gutbieri* Göppert, *Oligocarpia cliveri* H. Potonié, *Renaultia* sp., *Discopteris schumanni* Stur, and from a new genus and species of the Saar Carboniferous. According to Potonié (1960, p. 27) those from *Oligocarpia gutbieri* and from *O. cliveri* may be referred to, respectively, *Leiotriletes adnatus* (Kosanke) and *L. sphaerotriangulus* (Loose).

Leiotriletes inermis (Waltz) Ishchenko 1952

Plate 78, figs. 3, 4

1938 *Azonotriletes inermis* Waltz in Luber and Waltz, p. 11; pl. 1, fig. 3, pl. 5, fig. 58, and pl. A, fig. 2.

1952 *Leiotriletes inermis* (Waltz) Ishchenko, p. 9; pl. 1, figs. 2, 3.

1955 *Asterocalamotriletes inermis* (Waltz) Luber, p. 40; pl. 1, figs. 20, 21.

1955 *Leiotriletes inermis* (Waltz) Potonié and Kremp, p. 37.

Description of specimens. Spores radial, trilete; amb subtriangular, sides convex to almost straight, apices rounded. Laesurae distinct, simple, straight, extending almost to smooth equatorial margin. Exine 1–2 μ thick, laevigate.

Dimensions (50 specimens). Equatorial diameter 28–57 μ (mean 43 μ).

Previous records. From the Lower Carboniferous of the U.S.S.R.; Ishchenko (1958) indicates distribution from Devonian to Bashkirian.

Leiotriletes subintortus (Waltz) Ishchenko 1952 var. *rotundatus* Waltz 1941

Plate 78, figs. 5, 6

1941 *Azonotriletes subintortus* Waltz var. *rotundatus* Waltz in Luber and Waltz, pp. 13–14; pl. 2, fig. 15b.

1952 *Leiotriletes subintortus* (Waltz) Ishchenko var. *rotundatus* Waltz; Ishchenko, p. 11; pl. 1, fig. 7.

Description of specimens. Spores radial, trilete; amb subtriangular with rounded apices

EXPLANATION OF PLATE 78

All figures $\times 500$, and from unretouched negatives.

Figs. 1, 2. *Chaetosphaerites pollenisimilis* (Horst) Butterworth and Williams 1958. 1, Preparation P145C/2, 27.8 97.8 (L.939). 2, Preparation P145B/22, 36.1 103.2 (L.940).

Figs. 3, 4. *Leiotriletes inermis* (Waltz) Ishchenko 1952. 3, Proximal surface; preparation M811/5, 38.3 100.9 (L.941). 4, Proximal surface; preparation P034/1, 35.8 103.8 (L.942).

Figs. 5, 6. *L. subintortus* (Waltz) Ishchenko 1952 var. *rotundatus* Waltz 1941. 5, Proximal surface; preparation P163/6, 18.2 99.2 (L.943). 6, Proximal surface; preparation P163/7, 36.0 94.8 (L.944).

Figs. 7, 8. *L. ornatus* Ishchenko 1956. 7, Proximal surface; preparation P163/5, 29.3 106.2 (L.946). 8, Proximal surface; preparation P163/6, 39.0 95.9 (L.945).

Fig. 9. *L. curiosus* sp. nov. Holotype; proximal surface.

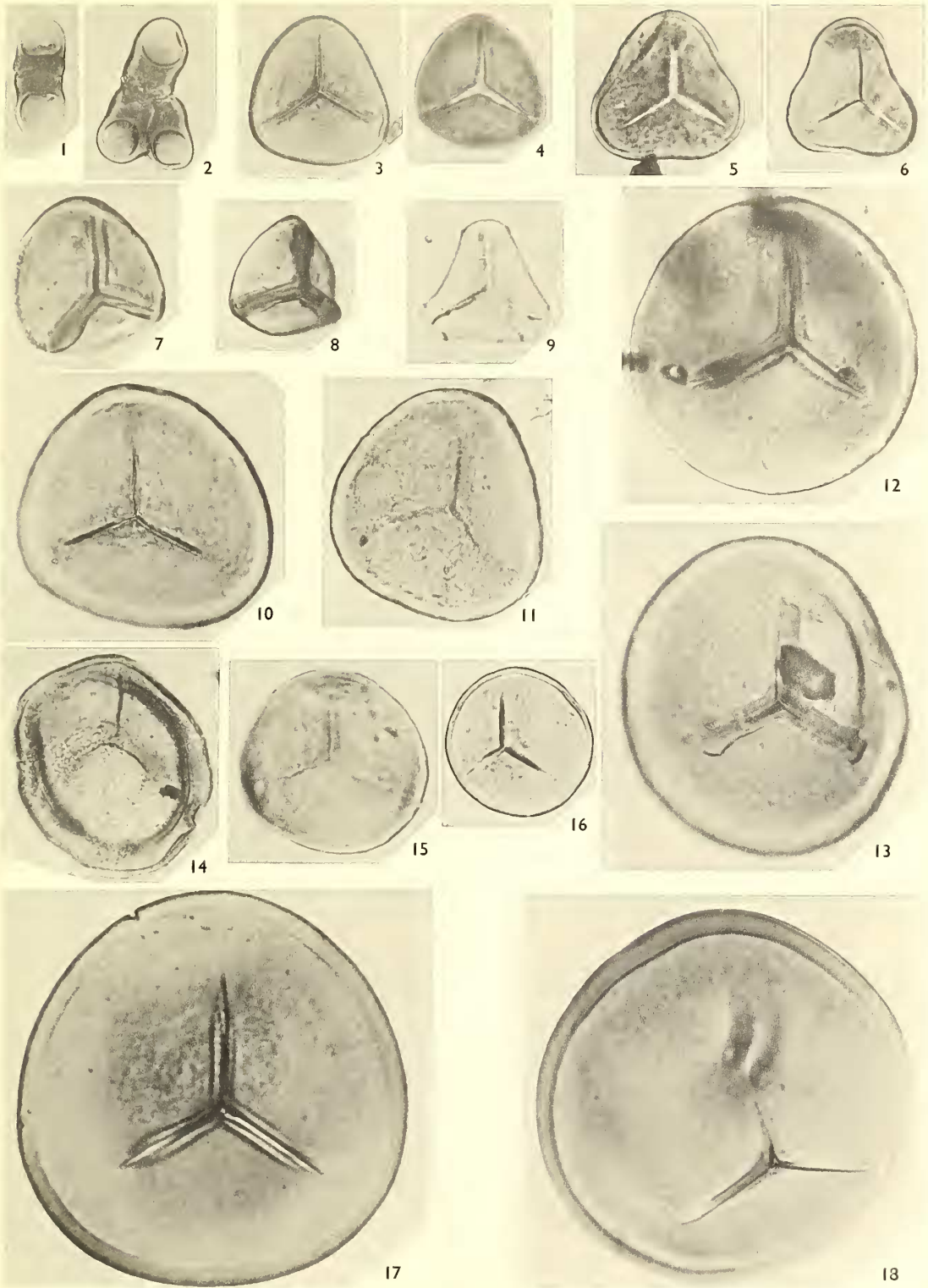
Figs. 10, 11. *L. microgranulatus* sp. nov. 10, Proximal surface; preparation P181/4, 52.3 112.4 (L.948). 11, Holotype; distal surface.

Figs. 12, 13. *Punctatisporites labiatus* sp. nov. 12, Holotype; proximal surface. 13, Proximal surface; preparation P163/5, 22.0 92.4 (L.957).

Fig. 14. *P. parvivermiculatus* sp. nov. Holotype; distal surface.

Figs. 15, 16. *P. glaber* (Naumova) comb. nov. 15, Proximal surface; preparation P148/1, 35.6 109.7 (L.952). 16, Proximal surface; preparation P163/5, 46.0 107.2 (L.953).

Figs. 17, 18. *P. pseudobesius* sp. nov. 17, Proximal surface; preparation P149A/31, 36.3 105.0 (L.960). 18, Holotype; proximal surface.



PLAYFORD, Lower Carboniferous microspores

and concave sides. Laesurae distinct, straight, simple, extending almost to smooth equatorial margin. Exine 1–2 μ thick, laevigate.

Dimensions (45 specimens). Equatorial diameter 26–50 μ (mean 38 μ).

Comparison. *Granulatisporites adnatus* Kosanke 1950 has a definite contact area, but *G. adnatus?* in Wilson and Hoffmeister (1956, p. 16; pl. 2, fig. 9) lacks this feature and is probably conformable with *L. subintortus* var. *rotundatus*.

Previous records. Apparently widespread in the Russian Lower Carboniferous, with previous records from Luber and Waltz (1941) and Ishchenko (1952, 1956, 1958), whose work indicates a range from Tournaisian to Bashkirian for this variety.

Leiotriletes ornatus Ishchenko 1956

Plate 78, figs. 7, 8

1956 *Leiotriletes ornatus* Ishchenko, p. 22; pl. 2, figs. 18–21.

1960 Spore type 1 of Love, p. 122; pl. 2, fig. 9 and text-fig. 12.

Description of specimens. Spores radial, trilete; amb subtriangular with convex to almost straight sides. Laesurae distinct, straight, length approximately equal to spore radius; with prominent, dark, raised lips individually 2.5–4.5 μ wide. Exine 2–3.5 μ thick, laevigate or occasionally sparsely infrapunctate (oil immersion).

Dimensions (55 specimens). Equatorial diameter 32–63 μ (mean 46 μ).

Comparison. The two specimens described by Love (1960, p. 122) are undoubtedly representative of this species; the apparent 'equatorial thickening' has been observed in a number of the Spitsbergen specimens, and, as suggested by Love, is the result of exinal folding due to compression. Spore type C of Neves (1958, p. 12; pl. 2, fig. 6) has an 'equatorial flange' according to the description, and the lips have considerably greater development than those of *L. ornatus*. *Filictriletes pyramidalis* (Luber in Luber and Waltz 1941, p. 54; pl. 12, fig. 182) Luber 1955 (p. 60; pl. 3, fig. 20) is larger than *L. ornatus* and appears to have only minor lip development.

Previous records. Ishchenko (1956) found this species to be restricted to Middle Viséan–Lower Namurian strata of the Western Donetz Basin. An interesting recent record is from the Pumpherstun Shell Bed (Viséan) of Scotland (Love 1960).

Leiotriletes microgranulatus sp. nov.

Plate 78, figs. 10, 11

Diagnosis. Spores radial, trilete; amb broadly roundly subtriangular. Simple, straight, distinct laesurae equal half to three-fifths of spore radius. Equatorial margin smooth. Exine 3–4.5 μ thick, finely and densely granulate ('peppery' appearance under oil immersion).

Dimensions (25 specimens). Equatorial diameter 58–86 μ (mean 70 μ).

Holotype. Preparation P176A/2, 23.5 95.2. L.947.

Locus typicus. Citadellet (sample G1451), Spitsbergen; Lower Carboniferous.

Description. Holotype subtriangular with slightly convex sides and broadly rounded apices, diameter $73\ \mu$; laesurae one-half spore radius; minutely granulate exine, $4\ \mu$ in thickness.

Comparison. *Leiotriletes convexus* (Kosanke 1950, pp. 20–21; pl. 3, fig. 6) Potonié and Kremp 1955 has similar sculpture but a thinner exine and longer laesurae.

Leiotriletes curiosus sp. nov.

Plate 78, fig. 9; text-fig. 5b

Diagnosis. Spores radial, trilete; amb subtriangular with straight to slightly concave sides and broad, bluntly rounded apices. Laesurae distinct, simple, straight or slightly undulating, length approximately four-fifths spore radius. Exine thin (less than $1\ \mu$), laevigate or faintly roughened (oil immersion). The (six) equatorial junctions between apical shoulders and interradial sides are each marked by a small, rounded, relatively broad-based granule.

Dimensions (25 specimens). Equatorial diameter, $28\text{--}40\ \mu$ (mean $35\ \mu$).

Holotype. Preparation P149B/1, 38·8 97·6. L.950.

Locus typicus. Triungen (sample G1470), Spitsbergen; Lower Carboniferous.

Description. Holotype $38\ \mu$; one laesura bordered by narrow folds simulating lips.

Remarks. On the basis of subtriangular shape and mainly smooth surface, this species is included within *Leiotriletes*, rather than in *Granulatisporites* which incorporates similarly shaped, but densely granulate spores.

GENUS PUNCTATISPORITES (Ibrahim) Potonié and Kremp 1954

Type species. *P. punctatus* Ibrahim 1933.

Affinity. Psilopsida, Filicineae, Cycadofilicineae? (after Potonié and Kremp 1955, p. 42; 1956b, p. 81).

Punctatisporites glaber (Naumova) comb. nov.

Plate 78, figs. 15, 16

1938 *Azonotriletes glaber* (Naumova) Waltz in Luber and Waltz, p. 8; pl. 1, fig. 2 and pl. A, fig. 3.

1952 *Leiotriletes glaber* (Waltz) Ishchenko, pp. 13–14; pl. 2, figs. 15, 16.

1955 *Calamospora glabra* (Naumova) Potonié and Kremp, p. 47.

1955 *Punctatisporites nitidus* Hoffmeister, Staplin, and Malloy, pp. 393–4; pl. 36, fig. 4.

1955 *Punctatisporites? callosus* Hoffmeister, Staplin, and Malloy, p. 392; pl. 39, fig. 7.

1956 *Leiotriletes glaber* Naumova; Ishchenko, pp. 18–19; pl. 1, figs. 7, 8.

1958 *Punctatisporites* cf. *nitidus* Hoffmeister, Staplin, and Malloy; Butterworth and Williams, p. 361; pl. 1, figs. 7, 8.

1960 *Punctatisporites curviradiatus* Staplin, p. 7; pl. 1, figs. 17, 20.

Description of specimens. Spores radial, trilete; equatorial outline circular. Laesurae distinct, simple, straight, length one-third to two-thirds spore radius. Exine $1.5\text{--}2\ \mu$ thick, laevigate (corroded specimens finely punctate); rarely folded.

Dimensions (38 specimens). Equatorial diameter $32\text{--}70\ \mu$ (mean $52\ \mu$).

Remarks. The above synonymy does not attempt to be exhaustive. Several other species, for example *Punctatisporites planus* Hacquebard 1957 (p. 308; pl. 1, fig. 12), may well prove to be conspecific with *P. glaber*. The intention, however, is to emphasize the multitudinous nomenclature prevailing among such simple, circular, laevigate spores, and particularly those occurring in the Carboniferous System. As these forms are apparently of limited stratigraphical value there seems little point in attempting a rigorous subdivision (particularly on the basis of minute variations in such few and simple morphological characters), and certainly the validity of naming a spore according to its stratigraphical horizon is extremely doubtful. It is, of course, recognized that the dispersed spores included within *P. glaber* are probably representative of several different plants.

Staplin (1960, p. 7) in discussing his new species *Punctatisporites curviradiatus* states that 'off-polar compression and resultant apparent curvature of two sutures distinguish this species from *P. nitidus* Hoffmeister, Staplin and Malloy'. This appears rather a questionable basis for specific distinction. The illustrations given by Waltz (*in* Lubert and Waltz 1938 and 1941) of *P. glaber* include identical spores showing this same feature. Comparison with Staplin's (1960) species is often difficult owing to the fact that relative terms only are used in stating the thickness of the spore wall (e.g. 'moderate').

Punctatisporites glaber (Naumova) comb. nov. was assigned to the genus *Calamospora* by Potonié and Kremp (1955, p. 47); however, its relatively thick, rarely folded exine, together with fairly extensive laesurae, indicate more appropriate inclusion within *Punctatisporites*.

Previous records. Numerous previous records from the Carboniferous (see synonymy above). According to Ishchenko (1958) this species ranges from Devonian to Bashkirian.

Punctatisporites parvivermiculatus sp. nov.

Plate 78, fig. 14; text-fig. 5k

Diagnosis. Spores radial, trilete; amb circular to subcircular. Laesurae distinct, more or less straight, equal three-quarters or more of spore radius, sometimes with incipient lips. Exine 2–3 μ thick; sculpture infravermiculate with very fine, shallow, short, anastomosing grooves indenting the otherwise laevigate spore wall, constituting a highly imperfect negative microreticulum.

Dimensions (30 specimens). Equatorial diameter 58–88 μ (mean 74 μ).

Holotype. Preparation P169/1, 31.3 98.1. L.954.

Locus typicus. Birger Johnsonfjellet (sample G1036), Spitsbergen; Lower Carboniferous.

Description. Holotype subcircular, equatorial margin undulating due to folding, diameter 68 μ ; laesurae slightly curved due to compression, length approximately three-quarters spore radius; exine 3 μ in thickness, with peripheral arcuate folds. In many specimens the nature of the exinal sculpture is evident only under oil immersion. The grooves never attain the dimensions necessary to delimit definite positive processes, such as verrucae or grana.

Comparison. *Punctatisporites vermiculatus* Kosanke 1950 (p. 19; pl. 2, fig. 4) is similar,

but has a thicker exine deeply incised by a more extensively developed vermiculate sculpture. Potonié and Kremp (1955, p. 104) considered that *P. vermiculatus* may perhaps be referable to *Camptotriletes*. However, *P. parvivermiculatus* sp. nov. with its relatively minor sculpture is more appropriately included within *Punctatisporites*.

Punctatisporites labiatus sp. nov.

Plate 78, figs. 12, 13

Diagnosis. Spores radial, trilete; amb circular. Laesurae straight, length two-thirds to three-quarters spore radius; emphasized by prominent, smooth, slightly raised lips, individually 3–4 μ wide. Exine 3–4.5 μ thick; laevigate to indistinctly infragranulate.

Dimensions (20 specimens). Equatorial diameter 69–113 μ (mean 88 μ).

Holotype. Preparation P163/1, 30.0 97.3. L.956.

Locus typicus. Birger Johnsonfjellet (sample G1089), Spitsbergen; Lower Carboniferous.

Description. Holotype circular, diameter 94 μ ; laesurae equal three-quarters spore radius, rimmed by pronounced, dark lips 4 μ wide; exine 3 μ thick, laevigate, not folded. Other specimens occasionally show minor peripheral folding.

Comparison. This species resembles *Punctatisporites flavus* (Kosanke 1950, p. 41; pl. 9, fig. 2) Potonié and Kremp 1955, but differs in having longer laesurae, with more pronounced and regular lip development. *Azonotriletes microrugosus* (Ibrahim) forma *karagandensis* Lubert (in Lubert and Waltz 1938, p. 22; pl. 5, fig. 56) is smaller with incipient lips and thinner, folded exine.

Punctatisporites pseudobesus sp. nov.

Plate 78, figs. 17, 18

Diagnosis. Spores radial, trilete; amb circular, oval or broadly roundly subtriangular. Laesurae distinct, straight, length one-half to two-thirds spore radius. Exine perceptibly infragranulate (oil immersion), thickness 5.5–8 μ (average 7 μ); folding infrequent.

Dimensions (35 specimens). Equatorial diameter 97–157 μ (mean 125 μ).

Holotype. Preparation P149A/22, 31.8 101.3. L.959.

Locus typicus. Triungen (sample G1470), Spitsbergen; Lower Carboniferous.

Description. Holotype circular, 121 μ in diameter, laesurae about three-fifths spore radius, exine 7 μ thick.

Comparison. The closely allied species, *Punctatisporites obesus* (Loose) Potonié and Kremp (1955, p. 43; pl. 11, fig. 124), has a thinner spore wall (up to 5 μ), somewhat shorter laesurae, and a different size range.

Punctatisporites stabilis sp. nov.

Plate 79, figs. 1, 2

Diagnosis. Spores radial, trilete, originally spherical; amb circular, practically smooth.

Laesurae distinct, simple, straight or slightly curved, length approximately three-quarters spore radius. Exine $1.5\text{--}2.5\ \mu$ thick; with distinct, minute (less than $1\ \mu$ across), shallow punctations scattered on both proximal and distal hemispheres. Exinal folding rare.

Dimensions (45 specimens). Equatorial diameter $63\text{--}94\ \mu$ (mean $76\ \mu$).

Holotype. Preparation P158/7, 31.5 114.5. L.962.

Locus typicus. Birger Johnsonfjellet (sample G1092), Spitsbergen; Lower Carboniferous.

Description. Holotype $90\ \mu$; exine $2.5\ \mu$ in thickness; punctae fairly uniformly distributed, *c.* $4\ \mu$ apart, occasionally slightly elongate forming short grooves up to $2\ \mu$ long.

Comparison. *Azonotriletes punctulatus* Waltz var. *giganteus* Waltz (in Lubert and Waltz 1941, p. 14; pl. 2, fig. 16a) appears similar to *Punctatisporites stabilis* sp. nov., but differs in having an oval outline, shorter laesurae and generally larger size ($90\text{--}115\ \mu$); closer comparison is difficult owing to the brevity of Waltz's description. Another rather similar species, *Punctatisporites punctatus* Ibrahim 1933 (Potonié and Kremp 1955, p. 45; pl. 11, figs. 122, 123), is distinguishable from *P. stabilis* on the basis of its longer laesurae, broadly roundly triangular amb, and infrapunctate sculpture.

Genus CALAMOSPORA Schopf, Wilson, and Bentall 1944

Type species. *C. hartungiana* Schopf in Schopf, Wilson, and Bentall 1944.

Affinity. Sphenophyllaceae?, Calamariaceae, Noeggerathiales (after Potonié and Kremp 1954, p. 123). Spores conformable with *Calamospora* have been reported by Kosanke (1955) from his homosporous Calamarian species *Mazostachys pendulata*; and by W. and R. Remy (1957) from *Noeggerathiostrubus vicinalis* E. Weiss, *Discinites* sp. cf. *bohemicus* K. Feistmantel, and *Discinites* sp. Spores which appear to closely resemble *Calamospora* were recovered by Walton (1957) from his new species *Protopytis scotica*, a fertile shoot from the Calciferous Sandstone Series (Lower Carboniferous) of Dunbartonshire, Scotland. On the evidence of *P. scotica*, Walton considered that *Protopytis* had peridophytic reproduction and proposed a new group, the Protopytiales, to include the genus.

Calamospora microrugosa (Ibrahim) Schopf, Wilson, and Bentall 1944

Plate 79, figs. 3, 4

1932 *Sporonites microrugosus* Ibrahim in Potonié, Ibrahim, and Loose, p. 447; pl. 14, fig. 9.

1933 *Laevigati-sporites microrugosus* (Ibrahim) Ibrahim, p. 18; pl. 1, fig. 9.

1938 *Azonotriletes microrugosus* (Ibrahim) Waltz in Lubert and Waltz, p. 10; pl. 1, fig. 1 and pl. A, fig. 1.

1944 *Calamospora microrugosa* (Ibrahim) Schopf, Wilson, and Bentall, p. 52.

1952 *Leiotriletes microrugosus* (Ibrahim) Ishchenko, p. 15; pl. 2, fig. 19.

1955 *Calamotriletes microrugosus* (Waltz) Lubert, p. 36; pl. 1, figs. 1-3.

Description of specimens. Spores radial, trilete, originally spherical; amb circular to subcircular (modified by folding). Laesurae distinct, straight, length one-half to two-thirds spore radius, sometimes with faint, narrow, lip development. Equatorial margin smooth. Exine very thin (usually less than $1\ \mu$); laevigate or very minutely granulate (oil immersion), characteristically strongly plicated with folds of both major and minor proportions.

Dimensions (40 specimens). Equatorial diameter 62–104 μ (mean 82 μ).

Remarks. Spores similar to *Calamospora microrugosa* have been designated by a variety of specific names, many clearly synonymous, but until a direct comparison of the types is possible more precise assignment of the above specimens is precluded. As noted by Potonié and Kremp (1955, p. 49), *Calamospora liquida* Kosanke 1950 is undoubtedly very close to *C. microrugosa*. This is also the case with various spores described and illustrated by Ishchenko (1952, 1956, 1958) as *Leiotriletes platirugosus* (Waltz 1941) with three varieties, *L. vetustus* Ishchenko 1952, *L. mitus* Ishchenko 1952, and *L. immanis* Ishchenko 1952. The latter two species were considered synonymous with *C. liquida* Kosanke by Dybová and Jachowicz (1957, p. 63). Potonié and Kremp (1955), Lubert and Waltz (1938, 1941), Naumova (1953), Ishchenko (1952, &c.), Lubert (1955), Bolkhovitina (1956, 1959), Chibrikova (1959), and Imgrund (1960) have all recorded *C. microrugosa* as such. Naumova (1953) notes the vertical range as Cambrian to Cretaceous.

Previous records. *C. microrugosa* has been recorded by numerous authors from the Carboniferous (see above).

GENUS PHYLLOTHECOTRILETES Lubert 1955

Type species. *P. nigrifellus* (Lubert) Lubert 1955.

Affinity. Unknown.

Phyllothecotriletes rigidus sp. nov.

Plate 79, figs. 5, 6

Diagnosis. Spores radial, trilete; amb circular to subcircular. Laesurae distinct, typically

EXPLANATION OF PLATE 79

All figures $\times 500$, and from unretouched negatives.

Figs. 1, 2. *Punctatisporites stabilis* sp. nov. 1, Holotype; proximal surface. 2, Proximal surface; preparation P158/7, 24.6 96.8 (L.963).

Figs. 3, 4. *Calamospora microrugosa* (Ibrahim) Schopf, Wilson and Bentall 1944. 3, Proximal surface; preparation P181/4, 40.4 112.6 (L.965). 4, Proximal surface; preparation P148/18, 44.8 111.8 (L.966).

Figs. 5, 6. *Phyllothecotriletes rigidus* sp. nov. 5, Holotype; proximal surface. 6, Proximal surface; preparation P176A/3, 22.8 97.4 (L.968).

Fig. 7. *Waltzispora lobophora* (Waltz) Staplin 1960. Distal surface; preparation P145A/1, 40.2 105.8 (L.970).

Figs. 8–11. *W. albertensis* Staplin 1960. 8, Proximal surface; preparation P145C/2, 46.7 112.9 (L.971). 9, Distal surface; preparation P145C/1, 48.4 100.1 (L.972). 10, Proximal surface; preparation P145B/30, 38.8 101.9 (L.973). 11, Proximal surface; preparation P145C/2, 52.3 98.1 (L.974).

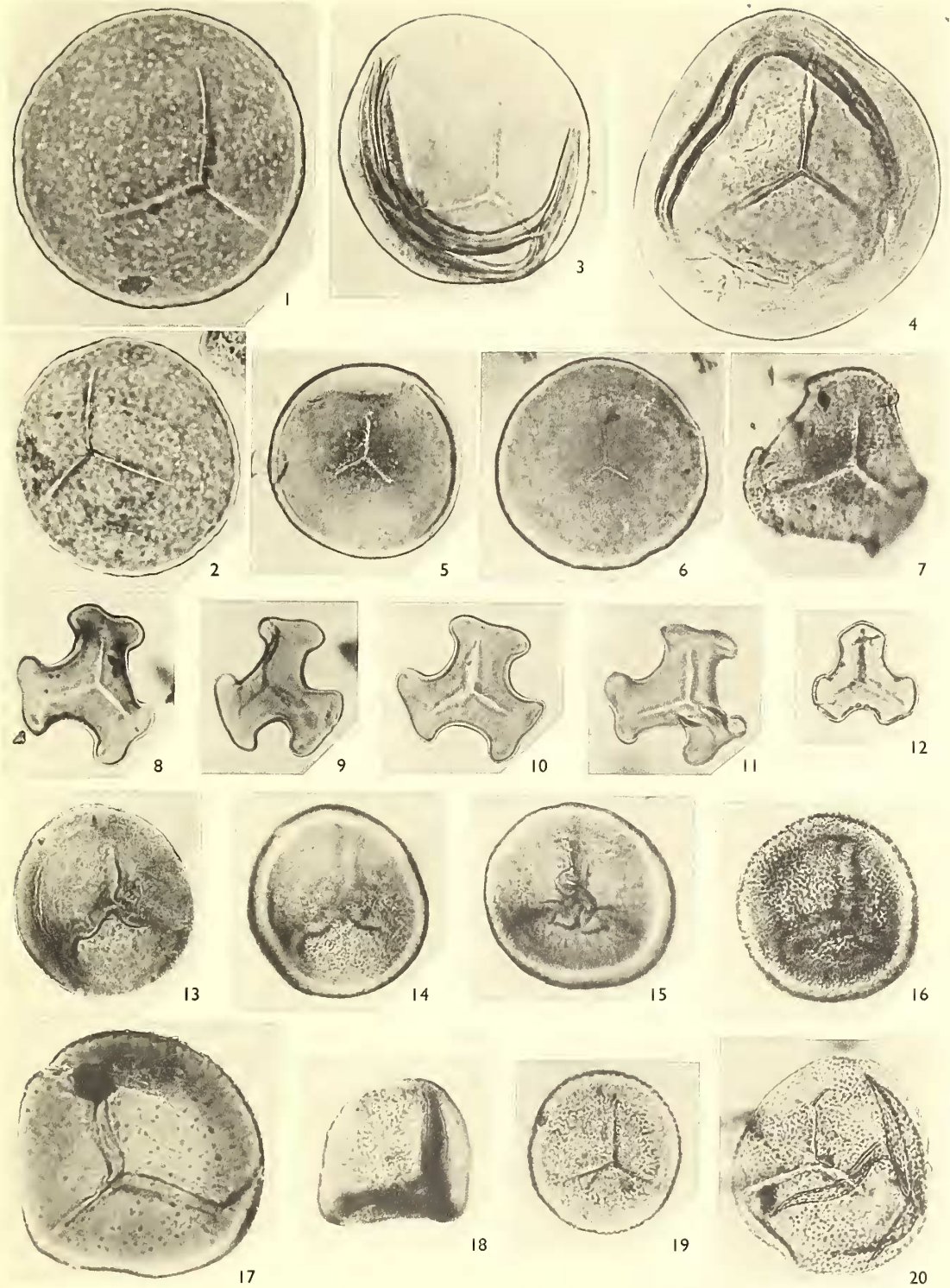
Fig. 12. *W. sagittata* sp. nov. Holotype; distal surface.

Figs. 13–16. *Cyclogranisporites flexuosus* sp. nov. 13, 14, Holotype; proximal and distal surfaces respectively. 15, Proximal surface; preparation P148/2, 45.8 94.0 (L.981). 16, Distal surface; preparation P148/33, 34.7 101.7 (L.982).

Fig. 17. *Lophotriletes coniferus* Hughes and Playford 1961. Proximal surface; preparation P175/7, 50.3 98.2 (L.993).

Fig. 18. *Granulatisporites planiusculus* (Lubert) comb. nov. Proximal surface; preparation P169/1, 33.9 113.5 (L.977).

Figs. 19, 20. *Cyclogranisporites lasius* (Waltz) comb. nov. 19, Proximal surface; preparation P175/2, 19.2 97.7 (L.978). 20, Proximal surface; preparation P145A/2, 22.4 112.2 (L.979).



PLAYFORD, Lower Carboniferous microspores

slightly sinuous; unequal in length, approximately one-third spore radius. Exine 2–4.5 μ thick, very finely granulate (oil immersion), folding minor—absent.

Dimensions (40 specimens). Equatorial diameter 57–77 μ (mean 66 μ).

Holotype. Preparation P172/3, 45.4 93.9. L.967.

Locus typicus. Citadelle (sample G1445), Spitsbergen; Lower Carboniferous.

Description. Holotype circular, 62 μ in diameter; exine 2.5 μ thick, very minutely granulate; laesurae \pm straight, approximately one-third spore radius, one slightly longer than others.

Comparison. *Phyllothecotriletes golatensis* Staplin 1960 (p. 9; pl. 1, fig. 27) is laevigate and has shorter laesurae; *P.?* *belloyensis* Staplin 1960 (p. 9; pl. 1, fig. 23) is smaller, and has longer laesurae together with distinct contact area.

Genus WALTZISPORA Staplin 1960

Type species. *W. lobophora* (Waltz) Staplin 1960.

Discussion. This distinctive genus embraces relatively simple, subtriangular, trilete spores having characteristically blunted and tangentially expanded radial extremities, and sculpture which, on presently known species, ranges from granulate to laevigate. It appears to have considerable stratigraphical significance within the Lower Carboniferous, as evidenced herein and from observations elsewhere.

Affinity. Unknown.

Waltzispora lobophora (Waltz) Staplin 1960

Plate 79, fig. 7

1884 Type 74 of Reinsch, p. 8; pl. 3, fig. 31.

1938 *Azonotriletes lobophorus* Waltz in Luber and Waltz, p. 12; pl. 1, fig. 5 and pl. A, fig. 8.

1941 *Azonotriletes lobophorus* Waltz var. *simplex* Waltz in Luber and Waltz, pp. 18–19; pl. 3, fig. 31.

1941 *Azonotriletes lobophorus* Waltz var. *submarginatus* Waltz in Luber and Waltz, pp. 18–19; pl. 3, fig. 32.

1956 *Triquitrites lobophorus* (Waltz) Potonié and Kremp, p. 87.

1960 *Waltzispora lobophora* (Waltz) Staplin, p. 18.

Description of specimens. Spores radial, trilete; amb subtriangular with concave to almost straight interrational margins, having conspicuous angular junctions with flatly rounded radial extremities, which thus constitute more or less prominent shoulders. Laesurae distinct, straight, length approximately four-fifths spore radius; sometimes with minor lip development in proximal polar region. Comprehensive granulate sculpture, particularly marked around distal pole, where grana are closely packed and comparatively large (up to 2.5 μ in basal diameter). Exine 1.5–2 μ thick.

Dimensions (20 specimens). Equatorial diameter 43–58 μ (mean 50 μ).

Remarks. The not extreme morphographical variation between specimens included within this species is clearly evident from the illustrations given by Reinsch (1884) and

by Lubert and Waltz (1938, and particularly 1941); it is confirmed by the Spitsbergen specimens recorded herein. In 1941 Waltz (*in* Lubert and Waltz, loc. cit.) distinguished two varieties of *Azonotriletes lobophorus*—var. *simplex* (identical to pl. 1, fig. 5 in Lubert and Waltz 1938) and var. *submarginatus*—which were not intended to be considered as discrete taxonomic units, but rather as extremes of infraspecific variation.

Comparison. If the absence of granules on the proximal surface is a constant feature of *Granulatisporites humerus* Staplin 1960 (p. 16; pl. 3, fig. 24) it may be considered as a species distinct from *W. lobophora* (Waltz). In any case, the inclusion of *G. humerus* within *Waltzisporea* is recommended on the basis of its close conformity to the type species in the diagnostic characters of equatorial outline and sculpture.

Previous records. This species was first reported by Reinsch (1884) from Russian (? Lower) Carboniferous rocks, and subsequently (Lubert and Waltz 1938, 1941) from the Lower Carboniferous of the Moscow Basin, and of the Selizharovo, Borovichi, and Kizel regions, U.S.S.R.

Waltzisporea albertensis Staplin 1960

Plate 79, figs. 8–11

1884 Type 78 of Reinsch p. 9; pl. 22, fig. 28A.

1957 cf. *Azonotriletes lobophorus* Waltz; Hacquebard and Barss, pp. 44–45; pl. 6, fig. 9.

1960 *Waltzisporea albertensis* Staplin, p. 18; pl. 4, figs. 2, 3.

Description of specimens. Spores radial, trilete. Amb concavely subtriangular, with prominent, blunted, radial extremities, which are conspicuously and more or less symmetrically expanded in a tangential direction; central parts of radial extremities often embayed (towards the polar axis). Laesurae more or less straight, length three-quarters to four-fifths spore radius; occasional minor development of lips. Exine 1.5–2 μ thick; essentially laevigate but may appear slightly roughened under oil immersion.

Dimensions (120 specimens). Equatorial diameter 23–37 μ (mean 29 μ).

Note that the discrepancy between the above size range and the measurements given by Hacquebard and Barss (1957) and Staplin (1960) is only apparent. Although not specified in their texts, it is evident from the plates that they have stated the 'angle to angle' measurement (Harris 1955, p. 14), whilst, as mentioned previously, the present writer takes the equatorial diameter of triangular forms as the maximum median length.

Remarks. The spores illustrated and described by Reinsch (1884) and Hacquebard and Barss (1957) as, respectively, type 78 and cf. *Azonotriletes lobophorus* Waltz 1938, are conformable in all respects with *W. albertensis* Staplin.

Previous records. This species has been recorded previously from the Russian (? Lower) Carboniferous (Reinsch 1884), and from the Upper Mississippian of Canada (Hacquebard and Barss 1957; Staplin 1960).

Waltzisporea sagittata sp. nov.

Plate 79, fig. 12; text-fig. 5c

1960 *Leiotriletes politus* (*non* Hoffmeister, Staplin, and Malloy 1955, p. 389; pl. 36, fig. 13) Love, pl. 1, fig. 1.

Diagnosis. Spores radial, trilete; amb subtriangular with concave interradial margins

and convex, somewhat pointed, radial extremities, which also show slight, but definite, tangential expansion. Laesurae simple, straight, length at least three-quarters spore radius. Equatorial margin smooth. Exine finely granulate to almost laevigate; up to $1\ \mu$ thick.

Dimensions (16 specimens). Equatorial diameter 24–35 μ (mean 29 μ).

Holotype. Preparation P180B/1, 54.4 105.8. L.975.

Locus typicus. Birger Johnsonfjellet (sample G1102), Spitsbergen; Lower Carboniferous.

Description. Holotype 27 μ ; proximal and distal surfaces with uniform sculpture of fairly widely spaced minute grana, which do not project at the equator; laesurae almost attain equatorial margin.

Comparison. *Waltzispora lobophora* (Waltz) Staplin 1960 is larger, more densely granulate, and the convexity of the radial extremities is less pronounced than in *W. sagittata* sp. nov. *Zonotriletes triplex* Andrejeva (*in* Luber and Waltz 1941, p. 18; pl. 3, fig. 33), which is almost certainly a comparatively thick-walled species of *Waltzispora*, is laevigate, has very deeply incised interradian margins, and ranges in size from 45 to 55 μ .

Remarks. The spore illustrated by Love (1960, pl. 1, fig. 1) as *Leiotriletes politus* (Hoffmeister, Staplin, and Malloy) appears identical to the Spitsbergen specimens described above, and seems to have little diagnostically in common with the description and illustration given by Hoffmeister, Staplin, and Malloy (1955, p. 389; pl. 36, fig. 13).

Although the photograph given by Butterworth and Williams (1958, pl. 1, fig. 15) is probably of a genuine representative of *Granulatisporites politus*, it is possible that *Waltzispora sagittata* sp. nov. is present in their Scottish material, but was considered by them as a variant of *G. politus*. This is suggested by the statement (Butterworth and Williams, loc. cit., p. 361) regarding 'the tendency for the rounded radial extremities to project laterally, thus giving an angular junction of radial and inter-radial areas', an attribute which suggested to them an analogy with a 'similar species', *Azonotriletes lobophorus* Waltz (which was subsequently designated as the type species of *Waltzispora*).

Previous records. From the Lower Oil-shale Group (Viséan) of Scotland (Love 1960).

Infraturma APICULATI (Bennie and Kidston) R. Potonié 1956

Subinfraturma GRANULATI Dybová and Jachowicz 1957

Genus GRANULATISPORITES (Ibrahim) Potonié and Kremp 1954

Type species. *G. granulatus* Ibrahim 1933.

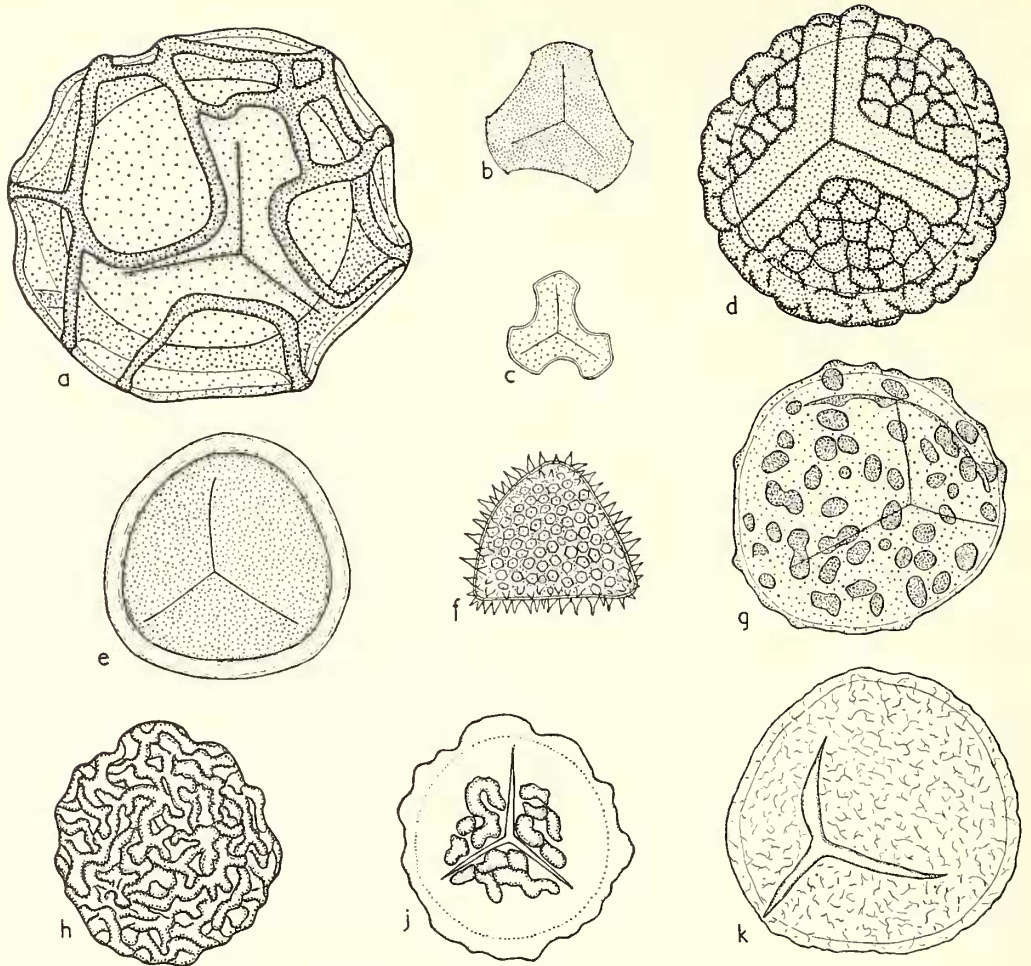
Affinity. Probably related to the Filices, and perhaps also to the Cycadofilicales (after Potonié and Kremp 1954, p. 126).

Granulatisporites planiusculus (Luber) comb. nov.

Plate 79, fig. 18

1955 *Filicitriletes planiusculus* Luber, p. 60; pl. 3, fig. 71.

Description of specimens. Spores radial, trilete; amb convexly subtriangular. Laesurae distinct, straight, extending to equatorial margin; prominent, dark, elevated lips,



TEXT-FIG. 5. Camera-lucida drawings; all magnifications $\times 500$ unless otherwise specified. *a*, *Reticulatisporites variolatus* sp. nov.; proximal surface; preparation P166/3, 32.9 98.1 (L.1047). *b*, *Leiotriletes curiosus* sp. nov.; proximal surface; preparation P149A/1, 20.4 102.4 (L.951). *c*, *Waltzisporea sagittata* sp. nov.; proximal surface; preparation P180B/2, 42.1 94.5 (L.976). *d*, *Verrucosisporites eximius* sp. nov.; proximal surface; preparation P149/A40, 35.5 109.5 (L.992). *e*, *Stenozonotriletes perforatus* sp. nov.; proximal surface; preparation P147A/1, 48.6 96.7 (L.1078). *f*, *Anapiculatisporites serratus* sp. nov.; distal surface; preparation P149A/2, 24.3 98.9 (L.1003). *g*, *Verrucosisporites gobbettii* sp. nov.; proximal surface; preparation P148/2, 17.0 109.7 (L.988). *h*, *j*, *Convolutispora harlandii* sp. nov. ($\times 250$); distal and proximal surfaces respectively; preparation P148/12, 34.9 103.1 (L.1019). *k*, *Punctatisporites parvivermiculatus* sp. nov.; proximal surface; preparation P163/6, 36.9 105.1 (L.955).

individually $2-3 \mu$ wide. Exine $2.5-3 \mu$ thick; distinctive, finely areolate sculpture with fairly regular, negative microreticulum encompassing fine, irregular granules.

Dimensions (15 specimens). Equatorial diameter $51-71 \mu$ (mean 60μ).

Remarks. The species is included within *Granulatisporites* on the basis of its subtriangular

amb and areolate-granulate sculpture. *Filicitriletes* Luber 1955 lacks type-species designation and in any case embraces the categories of several well-established genera (see Potonié 1958, p. 35).

Previous records. Luber (1955) recorded this species from the Lower (C1) and Upper (C3) Carboniferous of Kazakhstan.

Genus CYCLOGRANISPORITES Potonié and Kremp 1954

Type species. *C. leopoldi* (Kremp) Potonié and Kremp 1954.

Affinity. W. and R. Remy (1957, p. 61; pl. 3, fig. 11 and pl. 4, figs. 1–3) refer to *Microreticulatisporites* the microspores of *Noeggerathiostrubus bohemicus* O. Feistmantel (Upper Westphalian B), which, however, seem more closely related to *Cyclogranisporites*. Potonié (1960, p. 34) has noted the resemblance between *Cyclogranisporites* and the spores recovered by W. and R. Remy (1957, pl. 3, figs. 1, 2) from *Acitheca* (al. *Pecopteris*) *longifolia* Brongniart.

Cyclogranisporites lasius (Waltz) comb. nov.

Plate 79, figs. 19, 20

1884 Type 524 of Reinsch, p. 52; pl. 32, fig. 211 and pl. 42, fig. 220.

1938 *Azonotriletes lasius* Waltz in Luber and Waltz, p. 9; pl. 1, fig. 4 and pl. A, fig. 4.

1955 *Filicitriletes lasius* (Waltz) Luber, p. 55; pl. 2, fig. 50.

Description of specimens. Spores radial, trilete; amb circular. Laesurae simple, straight, length approximately two-thirds spore radius. Exine densely and finely granulate; thickness 1–3 μ .

Dimensions (20 specimens). Equatorial diameter 50–88 μ (mean 68 μ).

Remarks. *Filicitriletes* Luber 1955 was rejected correctly by Potonié (1958, p. 35) on the basis of its unsuitability as a generic unit, since it would embrace innumerable species already suitably placed in established genera. Potonié and Kremp (1955, p. 98) tentatively included *Azonotriletes lasius* Waltz within *Microreticulatisporites* (Knox) Potonié and Kremp. However, from the description given by Waltz (in Luber and Waltz 1938), the circular outline coupled with comprehensive granulate sculpture clearly indicates a correct assignment to *Cyclogranisporites*.

Previous records. Luber and Waltz (1938, 1941) and Luber (1955) have reported this species from the Lower Carboniferous of European Russia and of western Kazakhstan.

Cyclogranisporites flexuosus sp. nov.

Plate 79, figs. 13–16

Diagnosis. Spores radial, trilete; amb circular or subcircular, occasionally broadly roundly subtriangular. Laesurae approximately two-thirds to three-quarters amb radius, often totally obscured by prominent, raised, sinuous lips; overall width of lips up to 6.5 μ (usually about 3 μ), often varying considerably in any one specimen. Exine 3–5.5 μ thick; distal hemisphere sculptured with densely distributed fine grana; proximal hemisphere frequently with conspicuous laevigate-infragranulate contact faces, otherwise very finely granulate overall.

Dimensions (65 specimens). Equatorial diameter 44–78 μ (mean 59 μ).

Holotype. Preparation P148/1, 40·8 94·9. L.980.

Locus typicus. Triungen (sample G1472), Spitsbergen; Lower Carboniferous.

Description. Holotype subcircular, diameter 62 μ ; laesurae just perceptible, approximately two-thirds spore radius, straight, with strong, dark, sinuous lips individually 3 μ wide. Exine 5 μ thick; apart from laevigate contact faces, exine finely but conspicuously granulate.

Comparison. This species differs from other described representatives of *Cyclogranisporites* in its distinctively lipped laesurae together with thick exine.

Subinfraturma VERRUCATI Dybová and Jachowicz 1957

GENUS VERRUCOSISPORITES (Ibrahim) Potonié and Kremp 1954

Type species. *V. verrucosus* Ibrahim 1932.

Discussion. This genus and *Convolutispora* Hoffmeister, Staplin, and Malloy are closely related morphographically. *Verrucosisporites* is characterized by closely spaced verrucae whilst the sculpture of *Convolutispora* consists typically of crowded, anastomosing rugulae. Some difficulty is experienced in the generic assignment of species, e.g. *Convolutispora clavata* (Ishchenko), which possess composite rugulate/verrucate sculpture; in such instances the decision must rest upon an assessment of the predominating type of sculpturing elements.

Affinity. W. and R. Remy (1957) have recovered spores conformable with *Verrucosisporites* from the Upper Carboniferous fern fructifications *Corynepteris silesiaca* R. and W. Remy, *Zygopteris* sp., and *Waldenburgia corynepteroideis* Gothan.

Verrucosisporites gobbettii sp. nov.

Plate 80, figs. 1–4; text-fig. 5g

Diagnosis. Spores radial, trilete; amb circular to subcircular. Laesurae simple, straight, length two-thirds to three-quarters spore radius. Conspicuous sculpture of numerous, somewhat irregularly distributed verrucae, both discrete and coalescent, having circular to elliptical bases and broadly rounded apices; basal diameter of verrucae 4–12 μ (average 8 μ), height 2–3 μ . Surface between verrucae laevigate or very faintly infrapunctate; thickness of exine (excluding verrucae) 2 μ .

Dimensions (50 specimens). Equatorial diameter 55–89 μ (mean 72 μ).

Holotype. Preparation P148/42, 48·8 105·2. L.984.

Locus typicus. Triungen (sample G1472), Spitsbergen; Lower Carboniferous.

Description. Holotype circular, diameter 88 μ , amb undulating due to verrucae; laesurae distinct, equal three-quarters spore radius; one minor peripheral fold. Although comprehensive, the verrucate sculpture is, in most specimens, more pronounced on the distal hemisphere.

Comparison. *Verrucosisporites scrobiculatus* (Luber in Luber and Waltz 1938, p. 24;

pl. 5, fig. 70) Potonié and Kremp 1955 has more closely spaced, less broadly based projections, together with shorter laesurae. *V. baccatus* Staplin 1960 (p. 12; pl. 2, figs. 4, 10) has smaller sculpturing elements, shorter laesurae, and is additionally finely granulate.

The species is named for Dr. D. J. Gobbett of the Sedgwick Museum, Cambridge.

Verrucosisporites eximius sp. nov.

Plate 80, figs. 5-8; text-fig. 5d

Diagnosis. Spores radial, trilete, originally spherical; amb circular or subcircular. Laesurae distinct, straight, length three-quarters of, to almost equal to, amb radius; bordered by conspicuous, smooth lips extending 7-11 μ on either side. Exine strongly and comprehensively sculptured with large, flat-topped, closely packed, non-overlapping verrucae, which are separated by a continuous fine network of channels (up to 0.5 μ wide), i.e. constituting a negative microreticulum. Verrucae polygonal in surface view, 4-22 μ in longest diameter; normally smooth, but occasionally sparsely punctate (corroded specimens). Equatorial margin undulating. Exine very thick (5-8.5 μ , including sculpture).

Dimensions (30 specimens). Equatorial diameter 52-88 μ (mean 72 μ).

Holotype. Preparation P149A/36, 40.9 103.4. L.989.

Locus typicus. Triungen (sample G1470), Spitsbergen; Lower Carboniferous.

Description. Holotype 78 μ ; laesurae almost equal to spore radius; lips 8.5 μ wide, same height as polygonal verrucae; exine 7 μ in thickness. This species is characterized by its extremely thick, distinctively sculptured exine, together with pronounced development of lips.

Subinfraturma NODATI Dybová and Jachowicz 1957

Genus LOPHOTRILETES (Naumova) Potonié and Kremp 1954

Type species. *L. gibbosus* (Ibrahim) Potonié and Kremp 1954.

Affinity. Unknown.

Lophotriletes coniferus Hughes and Playford 1961

Plate 79, fig. 17

Dimensions (27 specimens). Equatorial diameter 69-105 μ (mean 89 μ).

Genus ANAPICULATISPORITES Potonié and Kremp 1954

Type species. *A. isselburgensis* Potonié and Kremp 1954.

Affinity. According to Potonié and Kremp (1955, p. 81) the genus may possibly be allied to the Filices.

Anapiculatisporites concinnus sp. nov.

Plate 80, figs. 9-12

Diagnosis. Spores radial, trilete; amb triangular with rounded apices and convex to

almost straight sides. Laesurae distinct, simple, more or less straight, length three-quarters to four-fifths spore radius. Proximal surface laevigate. Distal surface bearing scattered, small, uniform conii, $1-2\ \mu$ in length and $1-1.5\ \mu$ in basal diameter. Conii about $2-3\ \mu$ apart, fairly evenly distributed, but characteristically absent or markedly reduced in numbers at and around equatorial margin, particularly of interradial areas. Exine (excluding projections) about $1\ \mu$ thick; rarely folded. Equatorial margin mainly smooth with only a few projecting conii, and these generally in the vicinity of the triangular apices.

Dimensions (50 specimens). Equatorial diameter $23-44\ \mu$ (mean $32\ \mu$).

Holotype. Preparation P145C/1, 23.6 100.9. L.994.

Locus typicus. Triungen (sample G1466), Spitsbergen; Lower Carboniferous.

Description. Holotype $35\ \mu$; laesurae equal three-quarters spore radius; distal conii $1\ \mu$ broad at base, about $1.5\ \mu$ long, $2-4\ \mu$ apart, whole of proximal surface together with marginal interradial portions of distal surface entirely laevigate; twelve conii project from equator (four around each apex); margin otherwise smooth.

Comparison. This species is similar to *Granulatisporites? dumosus* Staplin 1960 (p. 16; pl. 3, figs. 15-17), which, however, differs principally in possessing spines that are 'largest along interradial portions of the equator' and 'reduced to granulations or absent at radial corners'; *G.? dumosus* should be assigned to *Anapiculatisporites*. In comparison with *Anapiculatisporites concinnus* sp. nov., *A. hispidus* Butterworth and Williams 1958 (p. 364; pl. 1, figs. 30, 31) has more prominent spinose ornamentation of different distribution, whilst *Azonotriletes cystostegius* Andrejeva (*in* Luber and Waltz 1941, p. 17; pl. 2, fig. 29) is sculptured with small, rounded tubercles. *Acanthotriletes microspinus* (*non* Ibrahim) Ishchenko 1958 (pp. 46-47; pl. 3, fig. 39) may be conspecific, at least in part, with *Anapiculatisporites concinnus*.

EXPLANATION OF PLATE 80

All figures $\times 500$ unless otherwise specified; from unretouched negatives.

Figs. 1-4. *Verrucosisorites gobbettii* sp. nov. 1, Holotype; distal surface. 2, Sub-polar view; preparation P226/2, 47.6 102.2 (L.985). 3, Proximal surface; preparation P181/2, 41.2 104.9 (L. 986). 4, Distal surface; preparation P176B/1, 27.7 112.9 (L.987).

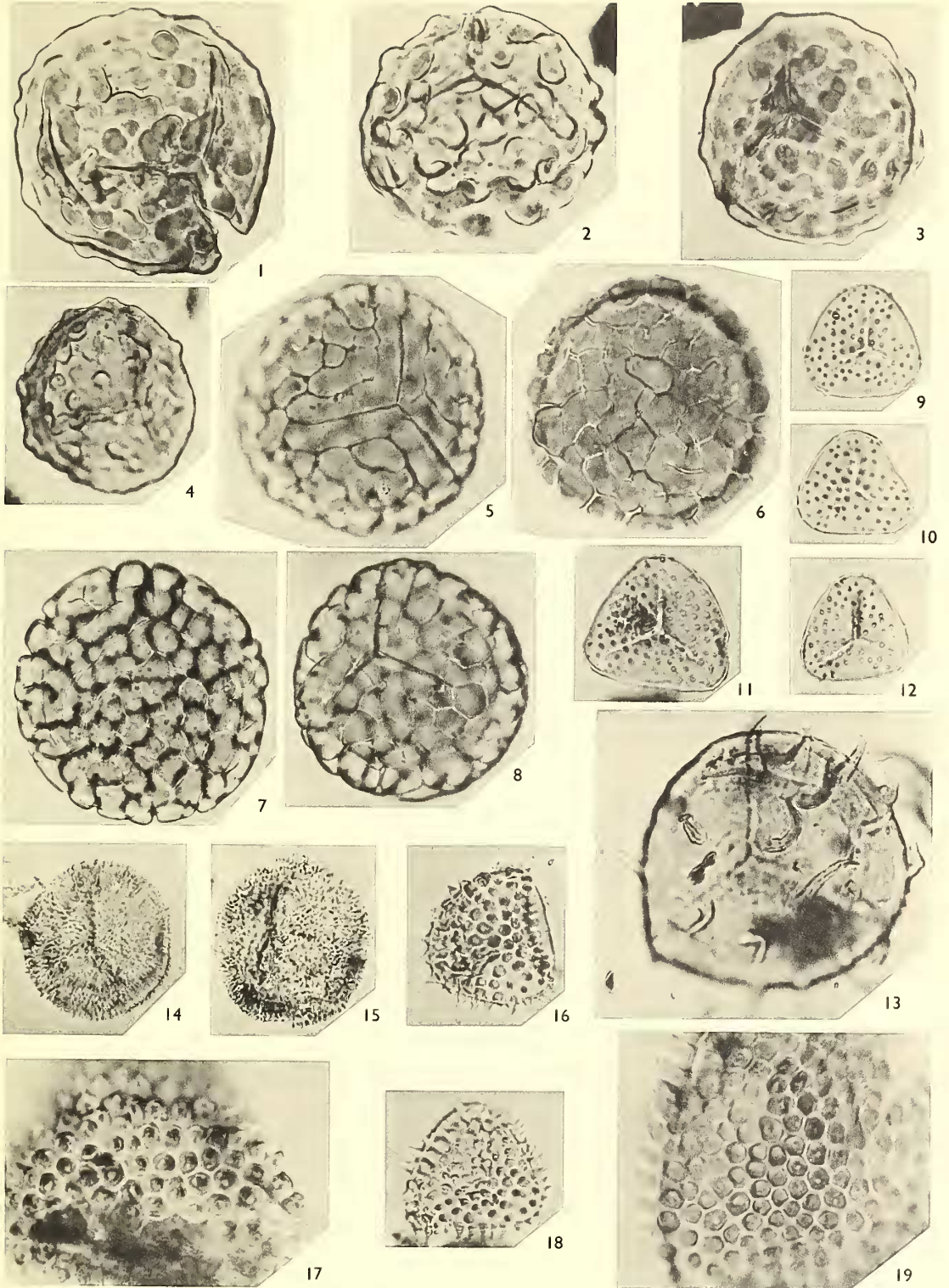
Figs. 5-8. *V. eximius* sp. nov. 5, 6, Holotype; proximal and distal surfaces respectively. 7, Sub-polar view; preparation P149A/11, 40.6 103.8 (L.990). 8, Proximal surface; preparation P149A/2, 46.8 106.3 (L.991).

Figs. 9-12. *Anapiculatisporites concinnus* sp. nov. 9, Holotype; distal surface. 10, Proximal surface; preparation P145B/37, 40.2 103.0 (L.995). 11, Proximal surface; preparation P164/3, 31.7 97.4 (L.997). 12, Distal surface; preparation P145B/2, 50.4 95.0 (L.996).

Fig. 13. *Hystricosporites* sp. Distal surface; preparation P164/1, 22.5 110.0 (L.1009).

Figs. 14, 15. *Acanthotriletes multisetus* (Luber) Potonić and Kremp 1955. 14, Proximal surface; preparation P175/2, 20.3 110.9 (L.1005). 15, Distal surface; preparation P163/1, 26.8 113.2 (L.1006).

Figs. 16-19. *Anapiculatisporites serratus* sp. nov. 16, Holotype; distal surface. 17, Closely spaced distal spinae having characteristic hexagonal bases, $\times 1,000$; preparation P145A/1, 44.8 108.4 (L.1000). 18, Distal surface; preparation P149A/2, 45.7 107.1 (L.1001). 19, Distal spinae, $\times 1,000$; preparation P145C/2, 40.2 113.3 (L.1002).



PLAYFORD, Lower Carboniferous microspores

Anapiculatisporites serratus sp. nov.

Plate 80, figs. 16–19; text-fig. 5f

1938 *Zonotriletes curiosus* (partim) Waltz in Luber and Waltz, pl. A, fig. 13 (non pl. 4, fig. 49).

Diagnosis. Spores radial, trilete; amb subtriangular with straight to slightly convex sides and rounded apices. Laesurae indistinct to perceptible, simple, straight, almost reaching to equatorial margin. Proximal surface laevigate. Distal surface strongly and uniformly sculptured with closely packed, broadly based, sharply tapering spines, which are also evident at the equator (projecting as a conspicuous pseudo-flange). Spines have characteristically hexagonal bases (diameter 2–4 μ) and range in length from 2.5 to 6 μ ; somewhat diminished in size and density around the triangular apices. Exine (excluding spinae) 1–1.5 μ thick.

Dimensions (15 specimens). Equatorial diameter (excluding spinae) 38–61 μ (mean 49 μ).

Holotype. Preparation P149A/3, 27.0 109.2. L.999.

Locus typicus. Triungen (sample G1470), Spitsbergen; Lower Carboniferous.

Description. Holotype 42 μ , convexly subtriangular. The species is characterized by its sculpture of strongly developed spines, which have distinctive hexagonal basal outlines (as seen in surface view) together with exclusively distal and equatorial distribution.

Remarks. The second spore figured in Luber and Waltz 1938 (pl. A, fig. 13) as *Zonotriletes curiosus* Waltz is almost certainly conspecific with *Anapiculatisporites serratus* sp. nov.; it undoubtedly represents a different species from the spore initially illustrated as *Zonotriletes curiosus* Waltz (in Luber and Waltz 1938, pl. 4, fig. 49) which, as reproduced in Luber and Waltz 1941 (pl. 5, fig. 79), has been utilized subsequently (Ishchenko 1956, 1958) as the reference type for *Z. curiosus*.

Comparison. *Procoronaspora williamsii* Staplin 1960 (p. 17; pl. 3, fig. 22) is smaller and has shorter laesurae; its spines are shorter at the distal pole, and do not possess the distinctive hexagonal bases of *Anapiculatisporites serratus*.

Genus APICULATISPORIS Potonié and Kremp 1956

Type species. *A. aculeatus* (Ibrahim) Potonié 1956.

Affinity. Unknown.

Apiculatisporis macrurus (Luber) Potonié and Kremp 1955

Plate 81, fig. 3

1938 *Azonotriletes macrurus* Luber in Luber and Waltz, p. 30; pl. 7, fig. 94.

1952 *Acanthotriletes macrurus* (Luber) Ishchenko, p. 28; pl. 6, fig. 65.

1955 *Apiculatisporites macrurus* (Luber) Potonié and Kremp, p. 77.

Description of specimens. Spores radial, trilete, originally spherical; amb circular to subcircular. Laesurae simple, length at least two-thirds spore radius; usually obscured by sculpture. Exine fairly thick, bearing prominent, somewhat variable, closely spaced

spines, which have more or less rounded apices, and are often fused at their bases; basal diameter of spines 3–6 μ , length 4.5–9 μ .

Dimensions (20 specimens). Equatorial diameter 50–65 μ (mean 59 μ).

Previous records. Reported previously from Russia only, as follows: from the Middle and Upper Carboniferous of the Donetz Basin (Luber and Waltz 1938, 1941; Ishchenko 1952); from Viséan–Namurian of the western extension of the Donetz Basin (Ishchenko 1956); and from Viséan–Bashkirian of the Dnieper–Donetz Basin (Ishchenko 1958).

Genus ACANTHOTRILETES (Naumova) Potonié and Kremp 1954

Type species. *A. ciliatus* (Knox) Potonié and Kremp 1954.

Affinity. W. and R. Remy (1957, p. 59; pl. 2, figs. 7–9) have recovered spores similar to *Acanthotriletes* from the Upper Carboniferous fern fructification *Sphyropteris* cf. *boehnischi* Stur.

Acanthotriletes multisetus (Luber) Potonié and Kremp 1955

Plate 80, figs. 14, 15

1938 *Azonotriletes multisetus* Luber in Luber and Waltz, p. 23; pl. 5, fig. 61.

1955 *Filicitriletes multisetus* (Luber) Luber, pp. 55–56; pl. 3, fig. 52.

1955 *Acanthotriletes multisetosus* (Luber) Potonié and Kremp, p. 84.

1957 *Acanthotriletes multisetus* (Luber) Kedo, p. 1167.

Description of specimens. Spores radial, trilete; equatorial outline circular to elliptical. Laesurae simple, obscure to perceptible, length approximately two-thirds spore radius. Exine thin (1–3 μ), commonly folded and torn; fine, dense sculpture of closely packed, minute projections which range from spinae to baculae and are evident at equator. Projections up to 1 μ in basal diameter and 2 μ in length, but usually considerably smaller.

Dimensions (30 specimens). Equatorial diameter 42–78 μ (mean 60 μ).

Comparison. *Cyclogranisporites amplus* McGregor 1960 (p. 26; pl. 11, fig. 8) is similar in general appearance, but larger and distinctly granulate.

Previous records. *Acanthotriletes multisetus* has been reported previously by Luber and Waltz (1938, 1941) and Luber (1955) from the Viséan of the Karaganda Basin; by Kedo (1957, 1958, 1959) from the Upper Tournaisian of White Russia; and recently by Love (1960) from the Lower Oil-shale Group (Viséan) of Scotland.

Acanthotriletes mirus Ishchenko 1956

Plate 81, figs. 1, 2

Description of specimens. Spores radial, trilete; amb circular to roundly subtriangular. Laesurae distinct, straight or slightly sinuous, length approximately equal to amb radius. Exine covered with numerous, evenly distributed, uniformly tapering spines, 4–8 μ high, 1.5–4 μ in basal diameter, and usually about 6 μ apart; remainder of surface somewhat rough in appearance (infrapunctate or infragranulate). Exine thickness (excluding spines) 2–3 μ .

Dimensions (12 specimens). Equatorial diameter 50–62 μ (mean 55 μ).

Previous records. Ishchenko (1956, stratigraphical range table 1) found this species to be restricted to Tournaisian strata of the Donetz Basin (western extension).

Genus HYSTRICOSPORITES McGregor 1960

Type species. *H. delectabilis* McGregor 1960.

Discussion. This genus was instituted by McGregor (1960, p. 31) to incorporate sub-circular spores possessing a proximal and distal sculpture of more or less uniformly tapering appendages bearing distinctive anchor-like apical terminations. As implied by McGregor, such spores would have undoubtedly found inclusion within the broad connotation of Naumova's (1953, p. 51) subgroup *Archaeotriletes*, which has since, however, been validated, emended, and thereby restricted by Potonié (1958, p. 30). McGregor discusses adequately the morphographical differences between *Archaeotriletes* (Naumova) Potonié 1958, *Nikitinisporites* Chaloner 1959, *Ancyrospora* Richardson 1960, and *Hystricosporites*, and they appear to represent clearly delineated generic units.

Affinity. Naumova (1953, pp. 8, 51) noted the resemblance between Devonian spores of her subgroup *Archaeotriletes*, and those of the present-day water fern *Azolla*. However, this similarity is probably only superficial (see McGregor 1960, p. 32).

Hystricosporites sp.

Plate 80, fig. 13

Description of specimens. Spores radial, trilete; amb broadly roundly subtriangular to subcircular. Laesurae distinct, length about three-quarters spore radius; accompanied by narrow, slightly elevated and convoluted, lips. Distal surface and equatorial region of proximal surface bear long, uniformly tapering processes, which have grapnel-like tips; length of processes 12–21 μ , basal diameter 4–6 μ . Exine 5–7 μ in thickness; micro-regularulate on proximal hemisphere, laevigate distally.

Dimensions (3 specimens). Equatorial diameter (excluding appendages) 88–119 μ .

Comparison. *Azonotriletes ancistrophorus* Luber (*in* Luber and Waltz 1941, p. 11; pl. 1, fig. 7; Luber 1955, p. 70; pl. 9, fig. 178), from the Upper Devonian and Lower Carboniferous of the U.S.S.R., is somewhat smaller (50–80 μ) and appears to lack a triradiate mark.

Remarks. The three spores described above, although insufficient to warrant the erection of a new species, represent an interesting new Lower Carboniferous occurrence of this distinctively sculptured group of spores, whose predominantly Devonian distribution is evident from Table 1 of McGregor (1960, p. 41). The only previous record from the Lower Carboniferous appears to be that of *Azonotriletes ancistrophorus* Luber, which occurs sparsely in Tournaisian strata of western Kazakhstan (Luber 1955).

Infraturma MURORNATI Potonié and Kremp 1954

Genus CONVOLUTISPORA Hoffmeister, Staplin, and Malloy 1955

Type species. *C. floridula* Hoffmeister, Staplin, and Malloy 1955.

Affinity. Unknown.

Convolutispora tuberculata (Waltz) Hoffmeister, Staplin, and Malloy 1955

Plate 81, figs. 4, 5

- 1938 *Azonotriletes tuberculatus* Waltz in Lubert and Waltz, p. 12; pl. 1, fig. 12, pl. 5, fig. 68, and pl. A, fig. 6.
 1955 *Verrucosporites tuberculatus* (Waltz) Potonié and Kremp, p. 66.
 1955 *Filicitriletes tuberculatus* (Waltz) Lubert, p. 54; pl. 2, figs. 45, 46.
 1955 *Convolutispora tuberculata* (Waltz) Hoffmeister, Staplin, and Malloy, p. 384.
 1956 *Lophotriletes tuberculatus* (Waltz) Ishchenko, p. 40; pl. 6, figs. 75, 76.

Description of specimens. Spores radial, trilete, originally spherical; amb circular to subcircular. Laesurae simple, straight, length one-third to two-thirds spore radius, usually obscured by sculpture. Exine relatively thick, uniformly sculptured with low, more or less rounded, closely packed, anastomosing ridges or irregular rugulae-verrucae; lumina relatively insignificant, very irregular; muri roughly 1.5–4.5 μ high, 2–5 μ broad, highly variable. Equatorial margin undulating.

Dimensions (50 specimens). Equatorial diameter 40–82 μ (mean 60 μ). Previous authors have recorded the following as equatorial diameter of this species: Waltz (in Lubert and Waltz 1938), 50–90 μ ; Lubert (1955), 60 μ ; Ishchenko (1956, 1958), 45–50 μ .

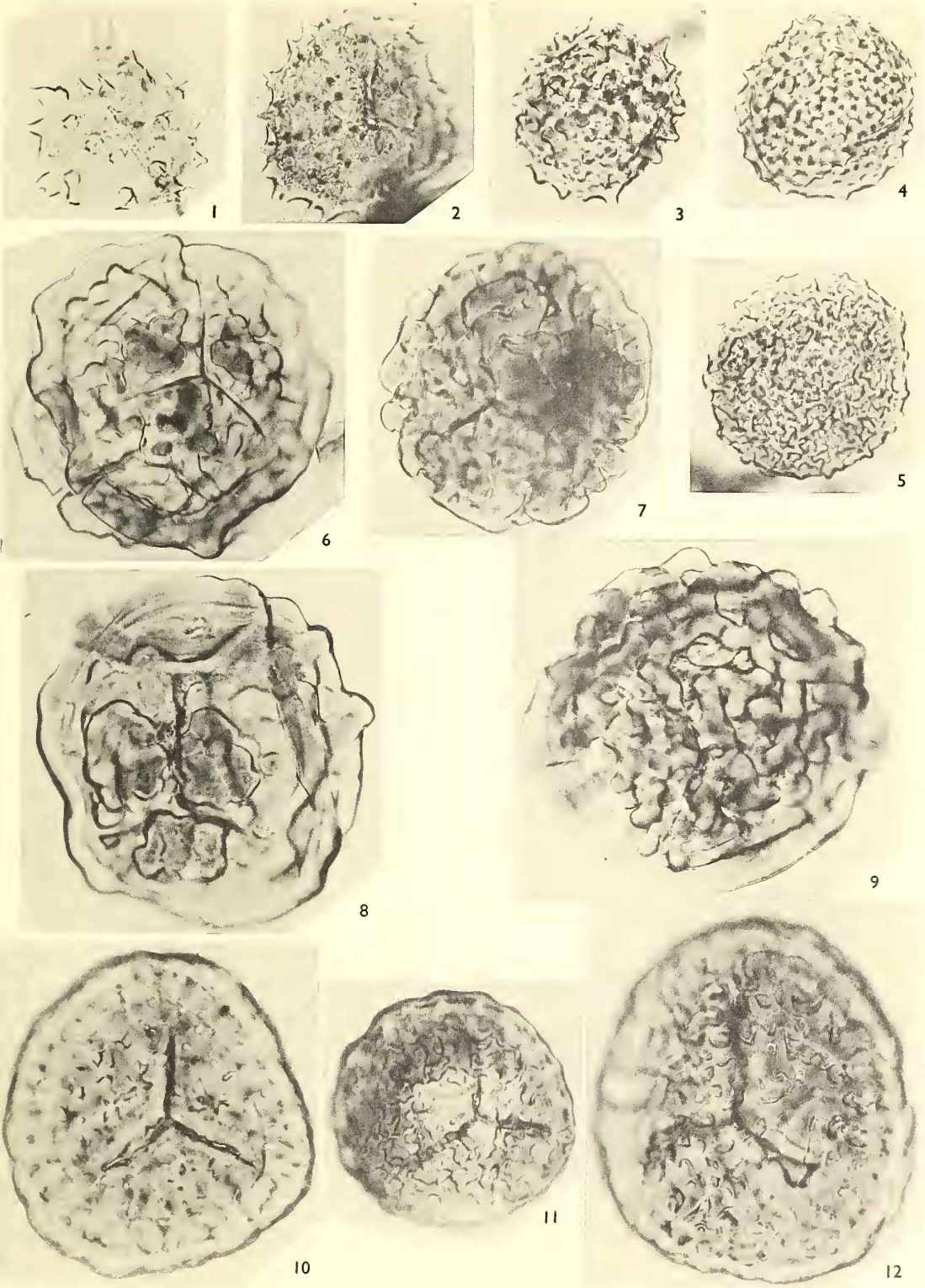
Comparison. The considerable variation, in both dimensions and sculpture, exhibited by this species was noted by Waltz (in Lubert and Waltz 1938) and although not precisely documented, is evident from her illustrations of *Azonotriletes tuberculatus*, and also from the specimens observed by the present writer. Two species described from North American strata of Mississippian age, *Convolutispora tessellata* Hoffmeister, Staplin, and Malloy 1955 (p. 385; pl. 38, fig. 9) and *C. punctatimura* Staplin 1960 (p. 12; pl. 2, figs. 12, 20, 21) appear to fall within this range of variation and are therefore probably synonymous with *C. tuberculata*.

Previous records. *Convolutispora tuberculata* has been reported by Lubert and Waltz (1938, 1941) from the Lower Carboniferous of the Moscow, Kizel, and Karaganda Basins, and the Voronezh region; by Lubert (1955) from the Lower Carboniferous of western Kazakhstan; and by Ishchenko (1956, 1958) from Upper Devonian–Namurian rocks of the Dnieper–Donetz Basin. Thus the Spitsbergen specimens described above are the first of this species reported definitely outside Russia.

EXPLANATION OF PLATE 81

All figures $\times 500$, and from unretouched negatives.

- Figs. 1, 2. *Acanthotriletes mirus* Ishchenko 1956. 1, Distal surface; preparation P226/4, 26.8 112.6 (L.1007). 2, Proximal surface; preparation P148/1, 46.1 101.5 (L.1008).
 Fig. 3. *Apiculatisporis macrurus* (Lubert) Potonié and Kremp 1955. Distal surface; preparation P163/1, 22.5 109.1 (L.1004).
 Figs. 4, 5. *Convolutispora tuberculata* (Waltz) Hoffmeister, Staplin, and Malloy 1955. 4, Sub-polar view; preparation P163/5, 18.4 110.7 (L.1011). 5, Distal surface; preparation P163/4, 34.3 103.2 (L.1012).
 Figs. 6–9. *C. harlandii* sp. nov. 6, Holotype; proximal surface. 7, Distal surface; preparation P148/15, 41.2 100.7 (L.1016). 8, Proximal surface; preparation P148/3, 38.7 100.5 (L.1017). 9, Distal surface; preparation P163/2, 21.2 113.8 (L.1018).
 Figs. 10–12. *C. crassa* sp. nov. 10, Proximal surface; preparation P148/1, 51.8 102.4 (L.1021). 11, Holotype; distal surface. 12, Distal surface; preparation P148/2, 44.8 92.9 (L.1022).



Convolutispora vermiformis Hughes and Playford 1961

Plate 82, figs. 5, 6

1957 *Convolutispora flexuosa* forma *minor* Hacquebard, p. 312; pl. 2, fig. 10.

Remarks. Spores recorded from Canada as *Convolutispora flexuosa* forma *minor* by Hacquebard (1957) and subsequently by McGregor (1960, p. 34; pl. 12, fig. 4) are considered identical to the Spitsbergen specimens which were described by Hughes and Playford (1961, p. 30; pl. 1, figs. 2–4) as *Convolutispora vermiformis*. As the spores almost definitely represent a distinct species, the latter name is retained in preference to the infraspecific taxon.

Dimensions (75 specimens). Equatorial diameter 47–86 μ (mean 66 μ). This corresponds closely to the size range of 47–81 μ noted by McGregor (1960) and includes the measurement (72 μ) stated by Hacquebard (1957).

Comparison. *Azonotriletes cancellothyris* Waltz (*in* Luber and Waltz 1941, p. 15; pl. 2, fig. 19) may be similar, but its description is too brief for precise comparison.

Previous records. Recorded previously from the Horton group (lowermost Mississippian) of Nova Scotia, Canada (Hacquebard 1957); from probable Upper Devonian of Melville Island, Canadian Arctic Archipelago (McGregor 1960); and from one sample (B685) of the Lower Carboniferous of Spitsbergen (Hughes and Playford 1961).

Convolutispora clavata (Ishchenko) Hughes and Playford 19611956 *Lophotriletes clavatus* Ishchenko, p. 43; pl. 6, fig. 82.1961 *Convolutispora clavata* (Ishchenko) Hughes and Playford, p. 31; pl. 1, figs. 7, 8.

Dimensions (30 specimens). Equatorial diameter 94–126 μ (mean 110 μ).

Previous records. Ishchenko (1956, 1958) described this species from Viséan sediments of the Donetz Basin (western extension) and of the Dnieper–Donetz Basin. Hughes and Playford (1961) reported its occurrence in the Spitsbergen Lower Carboniferous (sample S59a).

Convolutispora harlandii sp. nov.Plate 81, figs. 6–9; text-figs. 5*h, j*

Diagnosis. Spores radial, trilete; amb circular to subcircular, undulating. Laesurae distinct, simple, straight, length approximately two-thirds to three-quarters amb radius. Exine very thick (8–12 μ , including muri). Distal hemisphere with pronounced, convolute sculpture comprising a complex, tangled network of strongly developed, smooth, ramifying, sinuous, rounded muri, which are closely packed and overlapping; width of muri 6–10.5 μ ; lumina where delimited, irregular, usually elongate, up to 22 μ in longest diameter. Contact faces marked by three, discrete, interradial clusters of several, large, flattened, often fused, muri or rugulae-verrucae, which usually have a highly irregular outline in polar view; proximal hemisphere otherwise laevigate.

Dimensions (66 specimens). Equatorial diameter 73–140 μ (mean 106 μ).

Holotype. Preparation P163/7, 58.3 100.2. L.1015.

Locus typicus. Birger Johnsonfjellet (sample G1089), Spitsbergen; Lower Carboniferous.

Description. Holotype circular, diameter $100\ \mu$; laesurae two-thirds amb radius; exine $12\ \mu$ thick; distal surface with crowded, anastomosing ridges $6.3\text{--}8.5\ \mu$ wide; sculpture of proximal hemisphere restricted to contact areas, consisting of three relatively small, subequal areas, individually roughly $21\ \mu \times 17\ \mu$, resulting from the fusion of two or three low, irregular rugulae-verrucae. In some specimens included within this species, the muri in the equatorial region form a more or less continuous band (up to $18\ \mu$ wide), which although simulating a cingulum is, in fact, part of the sculptural pattern of the distal hemisphere. This species is named for Mr. W. B. Harland, of the Sedgwick Museum, Cambridge.

Convolutispora crassa sp. nov.

Plate 81, figs. 10–12

Diagnosis. Spores radial, trilete; amb convexly subtriangular to circular, gently undulating. Laesurae simple, straight, length two-thirds to three-quarters spore radius. Exine very thick ($8.5\text{--}16\ \mu$, including muri); comprehensive sculpture of closely spaced, relatively low, smooth, sinuous, flat-topped, non-overlapping muri, which both anastomose and terminate freely, constituting an imperfect reticulum. Breadth of muri highly variable ($2\text{--}11\ \mu$), height $1.5\text{--}3.5\ \mu$. Lumina irregular, often elongate, up to $20\ \mu$ in longest diameter.

Dimensions (35 specimens). Equatorial diameter $61\text{--}115\ \mu$ (mean $85\ \mu$).

Holotype. Preparation P163/6, 37.3 99.3. L.1020.

Locus typicus. Birger Johnsonfjellet (sample G1089), Spitsbergen; Lower Carboniferous.

Description. Holotype $79\ \mu$, subcircular; laesurae approximately three-quarters amb radius; exine $10.5\ \mu$ thick; muri $2\text{--}10\ \mu$ wide, $2.5\ \mu$ high; lumina $3\text{--}16\ \mu$ in longest diameter. The species is characterized by its exceptionally thick exine, which exhibits a distinctive, imperfectly reticulate sculpture.

Comparison. *Convolutispora crassa* sp. nov. is probably conspecific with *Zonotriletes planotuberculatus* Waltz (in Luber and Waltz 1941), but inadequate description (p. 21)

EXPLANATION OF PLATE 82

All figures $\times 500$, and from unretouched negatives.

Figs. 1–3. *Convolutispora labiata* sp. nov. 1, Holotype; proximal surface. 2, Proximal surface; preparation P158/7, 24.5 107.4 (L.1026). 3, Distal surface; preparation P158/10, 39.0 101.3 (L.1025).

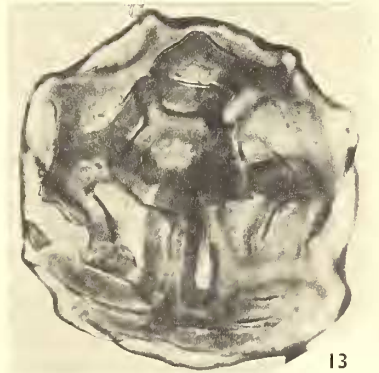
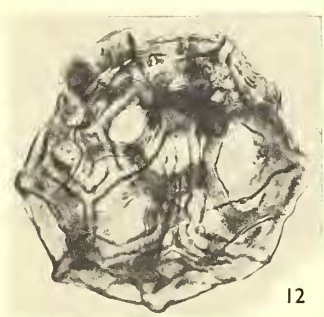
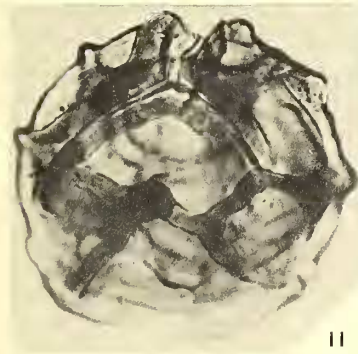
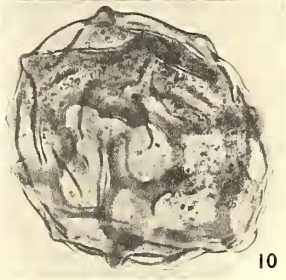
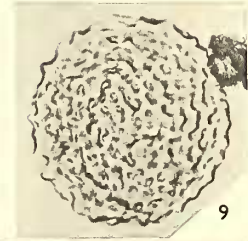
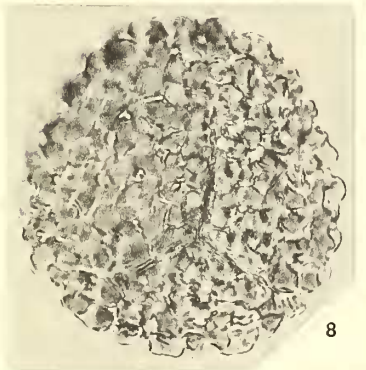
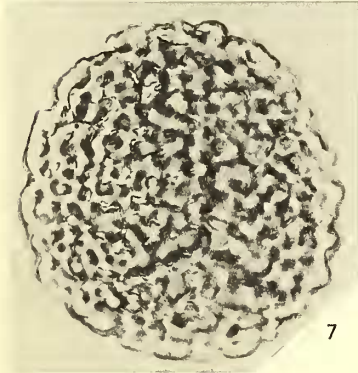
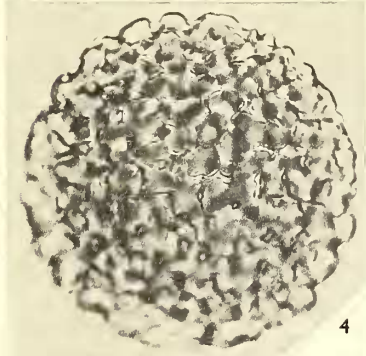
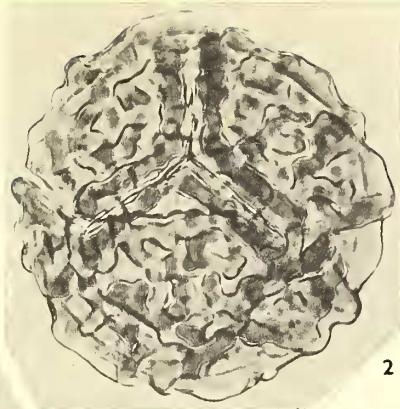
Figs. 4, 7, 8. *C. usitata* sp. nov. 4, Distal surface; preparation P149A/14, 39.9 102.6 (L.1029). 7, 8, Holotype; distal and proximal surfaces respectively.

Figs. 5, 6. *C. vermiformis* Hughes and Playford 1961. 5, Proximal surface; preparation P161B/3, 42.7 95.4 (L.1013). 6, Distal surface; preparation P163/4, 21.1 105.6 (L.1014).

Fig. 9. *Microreticulatisporites lunatus* Knox 1950. Distal surface; preparation P175/1, 32.4 92.9 (L.1031).

Fig. 10. *Reticulatisporites rudis* Staplin 1960. Proximal surface; preparation P145B/39, 38.5 103.7 (L.1036).

Figs. 11–13. *R. cancellatus* (Waltz) comb. nov. 11, Sub-polar view; preparation P163/8, 39.9 104.4 (L.1038). 12, Distal surface; preparation P139/3, 52.9 109.4 (L.1037). 13, Sub-polar view; preparation P163/4, 50.7 108.1 (L.1039).



and illustration (pl. 4, fig. 50) preclude an accurate comparison. Further, Waltz (loc. cit.) and subsequently Ishchenko, 1956 (who transferred the species to *Hymenozonotriletes* Naumova) did not mention a variation to subtriangular shape, and they apparently considered the species to be a zonate form, rather than one possessing an exceptionally thick spore wall. It should be added, however, that few Russian workers express adequately the distinction between a cingulum or zona, and a thick exine as seen in polar view (cf. discussion herein of *Stenozonotriletes*).

Previous records. The closely similar, if not identical, Russian species *Zonotriletes planotuberculatus* Waltz 1941 has been recorded by Luber and Waltz (1941) from the Lower Carboniferous of the Kizel region, and by Ishchenko (1956) who found it to be restricted to Tournaisian-Lower Viséan strata of the western Donetz Basin.

Convolutispora labiata sp. nov.

Plate 82, figs. 1-3

Diagnosis. Spores radial, trilete; amb circular to subcircular. Laesurae distinct, straight, length four-fifths of, to almost equal to, amb radius. Strongly developed, comprehensive sculpture of fairly closely spaced, rounded, smooth, sinuous muri, which both bifurcate and terminate freely. Width of muri irregular (range 3-12 μ), height 2-5 μ ; lumina rarely delimited. Prominent, more or less continuous lips result from radial alignment, and at least partial fusion, of muri in immediate vicinity of laesurae. Exine (including muri) 4.5-8 μ thick. Equatorial margin undulating.

Dimensions (20 specimens). Equatorial diameter 82-114 μ (mean 99 μ).

Holotype. Preparation P158/8, 36.0 103.3. L.1024.

Locus typicus. Birger Johnsonfjellet (sample G1092), Spitsbergen; Lower Carboniferous.

Description. Holotype 90 μ ; laesurae almost equal to spore radius, accompanied by mural lips (about 4 μ broad); convolute sculpture more strongly developed on distal surface but ridges remain non-overlapping; exine up to 6 μ thick.

Comparison. Although similar with respect to size and lip development, *Azonotriletes alveolatus* Waltz (in Luber and Waltz 1941, pp. 15-16; pl. 2, fig. 21) differs from *Convolutispora labiata* sp. nov. in having relatively narrow, uniform muri which coalesce to form a distinctly reticulate sculpture.

Convolutispora usitata sp. nov.

Plate 82, figs. 4, 7, 8

Diagnosis. Spores radial, trilete; originally spherical; amb circular or subcircular. Laesurae perceptible, simple, straight, length almost equal to spore radius. Exine 6-8 μ thick, including dense, comprehensive sculpture of broad, rounded, crowded, frequently anastomosing muri, 4-10 μ wide and 2-4 μ high; lumina highly irregular in shape and size, greatly subordinate to enclosing muri. Equatorial margin undulating to incised.

Dimensions (20 specimens). Equatorial diameter 84-112 μ (mean 100 μ).

Holotype. Preparation P149A/30, 36.7 102.5. L.1028.

Locus typicus. Triungen (sample G1470), Spitsbergen; Lower Carboniferous.

Description. Holotype diameter $91\ \mu$; laesurae $41\ \mu$ in length, discernible despite heavy exinal sculpture; exine $6.5\ \mu$ thick (including muri). The species possesses the typically 'convoluted' sculpture of the genus *Convolutispora*; its diagnostic features are large size, long laesurae, and strongly developed, ramifying muri.

Comparison. In comparison with *Convolutispora usitata* sp. nov., *C. cf. mellita* Hoffmeister, Staplin, and Malloy (Butterworth and Williams 1958, p. 372; pl. 2, figs. 20, 21) has shorter laesurae together with higher muri, which often fuse to form locally 'a thick, platy type of ornamentation'; *C. finis* Love 1960 (p. 115; pl. 1, fig. 7 and text-fig. 5) has much finer sculpture; and *C. clavata* (Ishchenko) Hughes and Playford 1961 (p. 31; pl. 1, figs. 7, 8) possesses shorter laesurae and less extensive, more verrucate sculpturing elements.

Genus MICRORETICULATISPORITES (Knox) Potonié and Kremp 1954

Type species. *M. lacunosus* (Ibrahim) Knox 1950.

Affinity. Unknown.

Microreticulatisporites lunatus Knox 1950

Plate 82, fig. 9

1948 Type 36K of Knox, fig. 41.

1950 *Microreticulatisporites lunatus* Knox, p. 320.

Description of specimens. Spores radial, trilete; amb circular, sinuous. Laesurae simple, straight, not always evident, length approximately equal to amb radius. Regular microreticulate sculpture of muri $1-2\ \mu$ wide and up to $1.5\ \mu$ high, enclosing rounded to polygonal lumina $2-4\ \mu$ in diameter. Exine (including muri) $2-3.5\ \mu$ thick.

Dimensions (36 specimens). Equatorial diameter $37-56\ \mu$ (mean $45\ \mu$). The mean corresponds with the single measurement given by Knox (1950, p. 320).

Previous records. From the Lower Carboniferous of Scotland (Knox 1948; Butterworth and Williams 1958).

Genus DICTYOTRILETES (Naumova) Potonié and Kremp 1954

Type species. *D. bireticulatus* (Ibrahim) Potonié and Kremp 1954.

Affinity. Unknown.

Dictyotriletes caperatus sp. nov.

Plate 83, figs. 3-5

Diagnosis. Spores radial, trilete; equatorial outline circular to subcircular. Laesurae distinct, straight, length three-fifths to two-thirds spore radius; often flanked by slightly raised, smooth, narrow lips about $2.5\ \mu$ wide, decreasing in width equatorially. Exine sculptured with very fine, narrow, sinuous muri, which are very low, thread-like, anastomosing or freely terminating to comprise an open-meshed reticulum imperfectum, inconspicuous in relation to overall proportions; lumina where delimited are of highly variable, usually irregular shape, ranging from 3 to $19\ \mu$ in diameter. Exine $3.5-6\ \mu$ thick; sometimes additionally infrapunctate or infragranulate.

Dimensions (40 specimens). Equatorial diameter 92–173 μ (mean 131 μ).

Holotype. Preparation P148/10, 37·9 104·1. L.1032.

Locus typicus. Triungen (sample G1472), Spitsbergen; Lower Carboniferous.

Description. Holotype 156 μ , amb elliptical due to compression; laesurae straight, approximately three-fifths spore radius, with smooth, narrow (3 μ) lips; exine finely, imperfectly reticulate, also infrapunctate; exine 4·5 μ thick, not folded. Some specimens show one or two major folds. Sculptural details are apparent only under oil.

Genus RETICULATISPORITES (Ibrahim) Potonié and Kremp 1954

Type species. *R. reticulatus* Ibrahim 1933.

Affinity. Spores conformable with *Reticulatisporites* have been recovered from *Sclerocelyplus oviformis* Mamay (1954, p. 82; pl. 21, figs. 7, 9). However, the systematic position of this Upper Carboniferous fructification is uncertain.

Reticulatisporites rudis Staplin 1960

Plate 82, fig. 10

Description of specimens. Spores radial, trilete, originally spherical; amb circular to subcircular. Laesurae distinct, simple, length approximately two-thirds spore radius. Conspicuous reticulate sculpture of smooth, rounded muri (2 μ broad at base, 2 μ high) enclosing polygonal lumina (7–14 μ in longest diameter). Exine (excluding muri) very finely granulate, 1·5–2 μ thick.

Dimensions (20 specimens). Equatorial diameter 59–73 μ (mean 66 μ).

Previous records. From the Golata formation (Upper Mississippian) of Alberta, Canada (Staplin 1960).

Reticulatisporites cancellatus (Waltz) comb. nov.

Plate 82, figs. 11–13; Plate 83, figs. 1, 2

1884 ? Type 555 of Reinsch, p. 54; pl. 38, fig. 271.

1933 ? Type F6 of Raistrick, p. 5.

1938 *Azonotriletes cancellatus* Waltz in Luber and Waltz, p. 11; pl. 1, fig. 8 and pl. 5, fig. 73.

1955 *Sphenophyllotriletes cancellatus* (Waltz) Luber, pp. 41–42; pl. 4, figs. 78a, b, 79.

1955 *Dictyotriletes cancellatus* (Waltz) Potonié and Kremp, p. 108.

1956 *Dictyotriletes cancellatus* (Waltz) Ishchenko, p. 45; pl. 7, figs. 88, 89.

1957 *Dictyotriletes cancellatus* (Waltz) Naumova; Kedo, p. 1166.

1957 *Reticulatisporites varioreticulatus* Hacquebard and Barss, p. 17; pl. 2, figs. 15, 16.

In discussing their new species *Reticulatisporites varioreticulatus*, Hacquebard and Barss (1957, p. 17) state justifiably that 'it could be conspecific with *Azonotriletes cancellatus* Waltz 1938, but the brevity of the description precludes a definite assignment'. However, further description and illustration of this species given subsequent to Luber and Waltz (1938), by Luber (1955) and by Ishchenko (1956, 1958), clarifies and somewhat broadens the concept of *Azonotriletes cancellatus*, and as such includes *Reticulatisporites varioreticulatus*.

Potonié and Kremp (1955, p. 108) listed *A. cancellatus* as a species of *Dictyotriletes* (Naumova) Potonié and Kremp. However, the prominent reticulate sculpture which is

often evident at the equator in the form of bastion-like projections (cf. Luber 1955, pl. 4, fig. 78; Ishchenko 1956, pl. 7, fig. 88) indicates more appropriate inclusion within *Reticulatisporites*.

Amplification of diagnosis. Spores radial, trilete; amb circular to subcircular. Laesurae usually distinct, length approximately two-thirds to three-quarters amb radius; bounded by flat, slightly elevated lips ($3-6\ \mu$ wide) having more or less straight outer margins. Prominent, comprehensive, fairly coarse, reticulate sculpture of smooth, rounded muri enclosing large, polygonal lumina. Muri $2.5-6.5\ \mu$ wide, up to $10\ \mu$ high, frequently expanded at their junctions, usually clearly evident in optical section as conspicuous projections at equator. Width of lumina $6-40\ \mu$, typically variable on individual specimens. Thickness of exine (excluding muri) $2-6\ \mu$.

Dimensions (100 specimens). Equatorial diameter $70-132\ \mu$ (mean $99\ \mu$). This corresponds closely to the size range of $75-130\ \mu$ stated by Ishchenko (1956, 1958) for *Dictyotriletes cancellatus* (Waltz).

Holotype. Plate 1, fig. 8 of Luber and Waltz 1938 (designated by Luber 1955).

Locus typicus. Kizel region, Verkhani-Goubakhine mine, Kalinine shaft, bed 7 (after Luber and Waltz 1938; Luber 1955).

Previous records. From the Lower Carboniferous of Russia (Luber and Waltz 1938, 1941, Luber 1955, Ishchenko 1956, 1958, and Kedo 1957, 1958), and of Canada (Hacquebard and Barsz 1957). Ishchenko (1958, stratigraphical range table 3) indicates that the species ranges from Upper Devonian to Viséan.

Reticulatisporites planus Hughes and Playford 1961

Plate 83, figs. 6, 7

Dimensions (40 specimens). Equatorial diameter $63-104\ \mu$ (mean $81\ \mu$). Based on an additional twenty-six specimens, this exceeds by $18\ \mu$ the upper limit of the size range stated by Hughes and Playford (1961, p. 31).

Reticulatisporites variolatus sp. nov.

Plate 84, figs. 5-8; text-fig. 5a

Diagnosis. Spores radial, trilete; originally spherical; amb circular to subcircular. Laesurae distinct to perceptible, straight, length one-half to three-quarters spore radius; simple or accompanied by narrow lip development. Comprehensively sculptured with smooth, strongly developed muri of more or less uniform width ($5-7\ \mu$) enclosing polygonal to irregularly rounded lumina ranging from 6 to $47\ \mu$ in longest diameter. Muri

EXPLANATION OF PLATE 83

All figures $\times 500$, and from unretouched negatives.

Figs. 1, 2. *Reticulatisporites cancellatus* (Waltz) comb. nov. 1, Distal surface; preparation P152/3, 44.4 111.8 (L.1041). 2, Proximal surface; preparation P148/3, 29.2 99.0 (L.1040).

Figs. 3-5. *Dictyotriletes caperatus* sp. nov. 3, Holotype; proximal surface. 4, Proximal surface; preparation P163/4, 49.7 93.9 (L.1033). 5, Sub-polar view; preparation P148/20, 34.7 106.1 (L.1034).

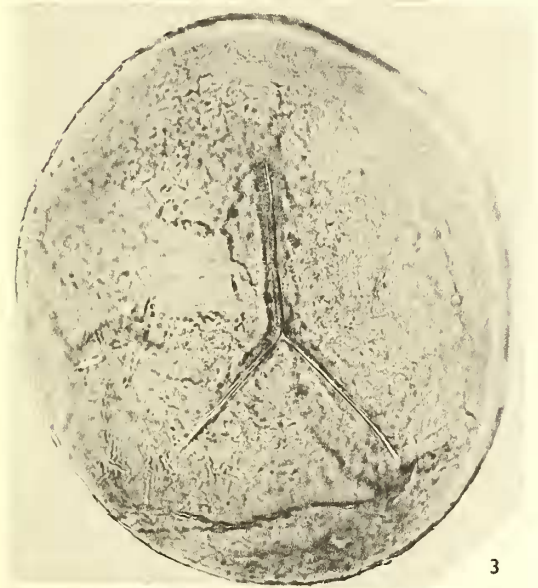
Figs. 6, 7. *Reticulatisporites planus* Hughes and Playford 1961. 6, Proximal surface; preparation P226/3, 39.5 101.0 (L.1043). 7, Distal surface; preparation P148/2, 35.1 94.8 (L.1042).



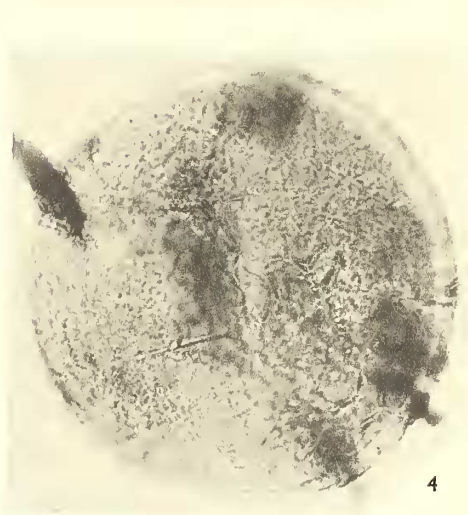
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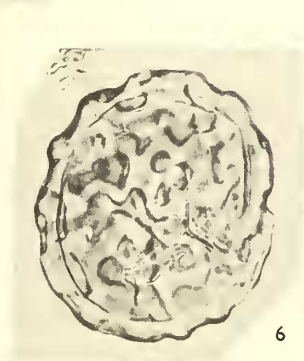
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7

4–8 μ high, with characteristic clavate (mushroom-shaped) profile. Exine very thick (9–12 μ , exclusive of muri); laevigate to finely punctate.

Dimensions (86 specimens). Equatorial diameter 77–124 μ (mean 98 μ).

Holotype. Preparation P165/3, 26.6 109.3. L.1044.

Locus typicus. Blårevbreen (sample Q55), Spitsbergen; Lower Carboniferous.

Description. Holotype subcircular, 108 μ in diameter; simple laesurae 29 μ long; coarsely reticulate with muri 6 μ high and 6.5 μ broad at top, enclosing lumina 10 μ –30 μ in longest diameter; exine 12 μ thick, excluding muri. In some specimens the lumina on the proximal hemisphere are markedly larger than those enclosed distally. The exceptionally thick spore wall may simulate a definite equatorial structure; its true nature is apparent, however, from a study of specimens compressed in orientations other than polar.

Comparison. *Reticulatisporites speciosus* Hacquebard and Barss 1957 (p. 18; pl. 2, fig. 17) is distinguishable on the basis of its exclusively distal, reticulate sculpture. *Euryzonotriletes semirotondus* (Waltz) Ishchenko 1956 (pp. 59–60; pl. 10, fig. 124) appears to represent a different species from that described and illustrated initially (Waltz in Lubert and Waltz 1941, p. 36; pl. 7, fig. 106), and may well be conspecific with *Reticulatisporites variolatus* sp. nov.

Previous records. Possibly recorded by Ishchenko (as above) from Tournaisian/Viséan strata of the western extension of the Donetz Basin.

Reticulatisporites peltatus sp. nov.

Plate 84, figs. 1–4

Diagnosis. Spores radial, trilete; originally spherical; amb circular to subcircular. Laesurae simple, straight, length almost equal to body radius; often obscured by sculpture. Exinal sculpture coarsely reticulate with smooth, rounded muri (2–5.5 μ wide and 2–3 μ high) enclosing irregularly polygonal lumina 6–46 μ in longest diameter (average 14 μ). Numerous, conspicuous, peltate (mushroom-like) processes are developed on, and characteristically at junctions of, the muri; processes 6–15 μ long (average 8 μ), 4–6.5 μ broad at base, (expanded) apices 5–13 μ in diameter; profile clearly evident at equator. Exine (exclusive of sculpture) 3.5–4.5 μ thick.

Dimensions (30 specimens). Equatorial diameter (excluding processes) 50–105 μ (mean 77 μ).

Holotype. Preparation P167B/14, 36.2 102.9. L.1048.

Locus typicus. Birger Johnsonfjellet (sample G1098), Spitsbergen; Lower Carboniferous.

Description. Holotype subcircular, body diameter 90 μ , laesurae distinct and long; muri 5 μ broad, 3 μ high; peltate processes up to 10 μ long and 11 μ wide at top; exine (excluding sculpture) 4 μ thick. Width of muri and length of processes are typically fairly uniform on any one specimen.

Comparison. This species is similar in construction to *Raistrickia boleta* Staplin 1960

(p. 14; pl. 2, figs. 25, 27), but differs in being more definitely and regularly reticulate, and in possessing longer laesurae together with less coarse, more uniform, and generally shorter accessory projections. Closer comparison is difficult, however, owing to the brevity of Staplin's description, and the evident corrosion of his illustrated specimens.

Reticulatisporites? sp.

Plate 85, figs. 1, 2

Description of specimens. Spores radial, trilete. Equatorial outline of body subtriangular with concave sides and rounded apices; interradial concavity often pronounced. Laesurae distinct, simple, straight, length approximately three-quarters body radius. Comprehensively sculptured with very high, narrow, membranous muri which ramify to form an irregular, wide-meshed reticulum. Equatorial muri simulate a broad flange extending outwards as much as $32\ \mu$; proximal and distal muri flattened due to compression. Muri approximately $1\ \mu$ wide; their greater part frequently lost in preservation and/or preparation, but junctions often persist as saetae-like projections. Exine (excluding sculpture) $3.5\text{--}5\ \mu$ around apices, $2\text{--}3\ \mu$ elsewhere.

Dimensions (9 specimens). Equatorial diameter of body $59\text{--}66\ \mu$ (mean $63\ \mu$).

Remarks. This unusual species appears distinct from any previously described representatives of the Murornati. Its inclusion within *Reticulatisporites* is tentative, since it is not entirely conformable with that genus. Although not stated in the formal emendation (Potonié and Kremp 1954, p. 144) of *Reticulatisporites*, most authors (e.g. Schopf, Wilson, and Bentall 1944, p. 44; Hoffmeister, Staplin, and Malloy 1955*b*, p. 395; Bhardwaj 1957, p. 121) consider circular or subcircular amb as a diagnostic attribute of the genus. Moreover, the exceptionally high, membranous muri together with slight exinal thickening at the apices seem unusual for *Reticulatisporites*. Thus the erection of a new genus may later become justified, dependent upon the discovery of further specimens similar, if not identical, to those described above. The nine specimens here recorded are, however, considered insufficient for the institution of even a formally named species. Similarity exists between this species and spores of the *Selaginella megastachys* group figured by Knox (1950, pl. 12, figs. 90–97).

Genus FOVEOSPORITES Balme 1957

Type species. *F. canalis* Balme 1957.

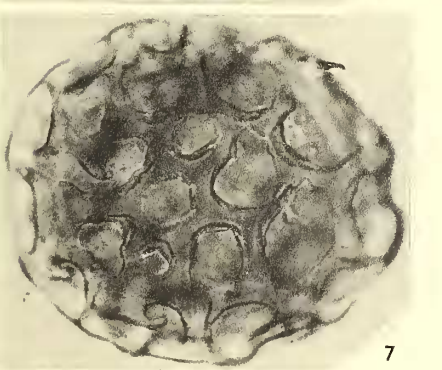
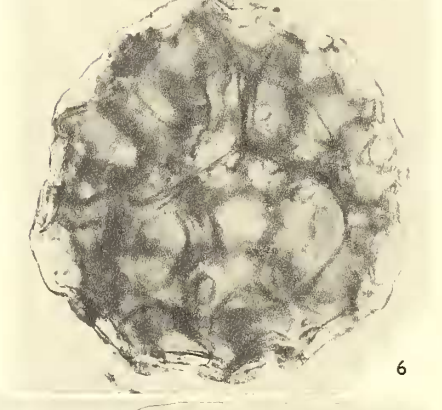
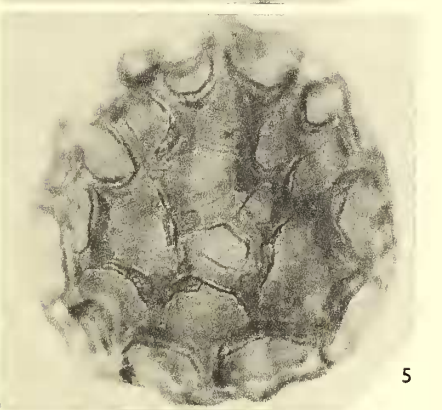
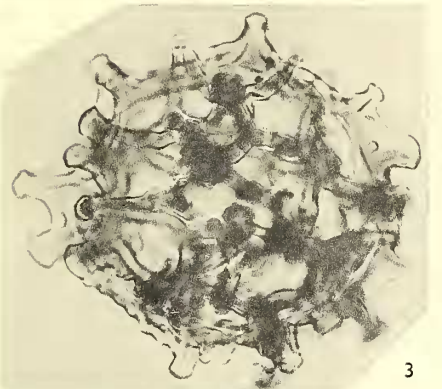
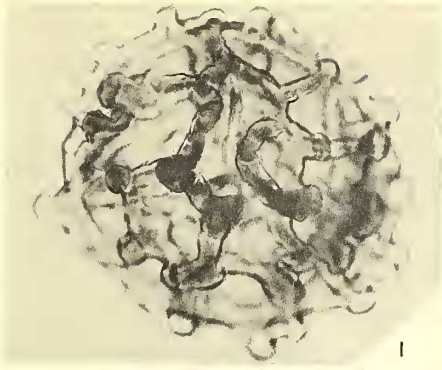
Discussion. This genus was instituted by Balme (1957, p. 17) for the reception of circular or roundly triangular trilete spores possessing a sculpture of 'pits or short channels

EXPLANATION OF PLATE 84

All figures $\times 500$, and from unretouched negatives.

Figs. 1–4. *Reticulatisporites peltatus* sp. nov. 1, 2, Holotype; distal and proximal surfaces respectively. 3, Distal surface; preparation P145B/41, $37.6\ 102.7$ (L.1049). 4, Distal surface; preparation P179/1, $33.2\ 102.8$ (L.1050).

Figs. 5–8. *R. variolatus* sp. nov. 5, 6, Holotype; distal and proximal surfaces respectively. 7, Distal surface; preparation P165/3, $54.4\ 97.9$ (L.1045). 8, Proximal surface; preparation P165/2, $43.7\ 101.6$ (L.1046).



irregularly distributed'. Although the type species is from the Mesozoic (of Western Australia), there is no justification for erecting a new genus to include Palaeozoic spores, such as the species described below, which conform with the diagnosis of *Foveosporites*.

Affinity. Balme (loc. cit.) has pointed out the resemblance between *F. canalis* and spores of the *Lycopodium verticillatum* group, which were described and illustrated by Knox (1950, pp. 227–8; pl. 9, figs. 44–48).

Foveosporites insculptus sp. nov.

Plate 85, figs. 3–5

Diagnosis. Spores radial, trilete; amb circular to subcircular; originally spherical. Laesurae distinct, simple, straight or slightly curved, length three-fifths to four-fifths spore radius. Exine has prominent, comprehensive sculpture of sharply defined, irregularly distributed punctae, together with very narrow grooves, which often bifurcate but never coalesce to the extent of constituting a negative reticulum; depth of incisement up to $2\ \mu$. Thickness of exine $3\text{--}5.5\ \mu$. Equatorial margin slightly indented.

Dimensions (35 specimens). Equatorial diameter $63\text{--}97\ \mu$ (mean $78\ \mu$).

Holotype. Preparation P149A/7, 35.8 102.3. L.1054.

Locus typicus. Triungen (sample G1470), Spitsbergen; Lower Carboniferous.

Description. Holotype $71\ \mu$, circular; laesurae $28\ \mu$ long; exine $4\ \mu$ thick, with characteristic, discontinuous, punctate/vermiculate sculpture.

Comparison. This species is distinguishable from *Punctatisporites parvivermiculatus* sp. nov. in its relatively coarse sculpture and thicker exine. Another similar species occurring in the Spitsbergen material, *Punctatisporites stabilis* sp. nov., is essentially punctate and has a thinner spore wall than *Foveosporites insculptus* sp. nov. *Punctatisporites vermiculatus* Kosanke 1950 (p. 19; pl. 2, fig. 4) has a thicker exine, rather indistinct laesurae, together with wider, more deeply incised grooves which appear to form a fairly well-developed network.

Subturma PERINOTRILITES Erdtman 1947
Genus PEROTRILITES (Erdtman) ex Couper 1953

Type species. *P. granulatus* Couper 1953.

Discussion. Balme and Hassell (1962, p. 20) assigned to their new genus *Diaphanospora* some Australian Upper Devonian spores which they stated 'could be placed, on purely morphographic grounds, in the genus *Perotriletes* [*sic*] (Erdtman) ex Couper'. The apparent absence of such perinate forms in the Permian and Triassic of Australia is not considered sufficient justification for their assignment to a form genus other than *Perotrilites*. *Perotrilites* of Devonian age was reported earlier by McGregor (1960, p. 35).

Affinity. Spores of the Recent *Selaginella sibirica* group figured by Knox (1950, pl. 11, figs. 76–82) appear conformable with *Perotrilites*.

Perotrilites perinatus Hughes and Playford 1961

Plate 85, figs. 6, 7

Dimensions (80 specimens). Diameter of spore body 44–90 μ (mean 70 μ).

Comparison. The spores figured and described briefly by Balme (1960, p. 29; pl. 4, figs. 18, 19) as *Auroraspora* sp., from the Laurel Beds (Lower Carboniferous) of the Fitzroy Basin, Western Australia, are perhaps conspecific with *P. perinatus*. *Diaphanospora riciniata* Balme and Hassell 1962 (p. 22; pl. 4, figs. 1–4; text-fig. 5) has pronounced lip development and its central body wall is equatorially thickened.

Perotrilites magnus Hughes and Playford 1961

Plate 85, fig. 8

Dimensions (55 specimens). Diameter of spore body 97–160 μ (mean 125 μ).

Turma ZONALES (Bennie and Kidston) R. Potonié 1956
 Subturma AURITOTRILETES Potonié and Kremp 1954
 Infraturma AURICULATI (Schopf) Potonié and Kremp 1954
 Genus TRIQUITRITES (Wilson and Coe) Potonié and Kremp 1954

Type species. *T. arcuatus* Wilson and Coe 1940.

Affinity. Definite evidence of the botanical affinity of this distinctive group of spores appears to be lacking. Schopf, Wilson, and Bentall (1944, p. 46) have suggested a possible filicean relationship.

Triquitrites trivalvis (Waltz) Potonié and Kremp 1956

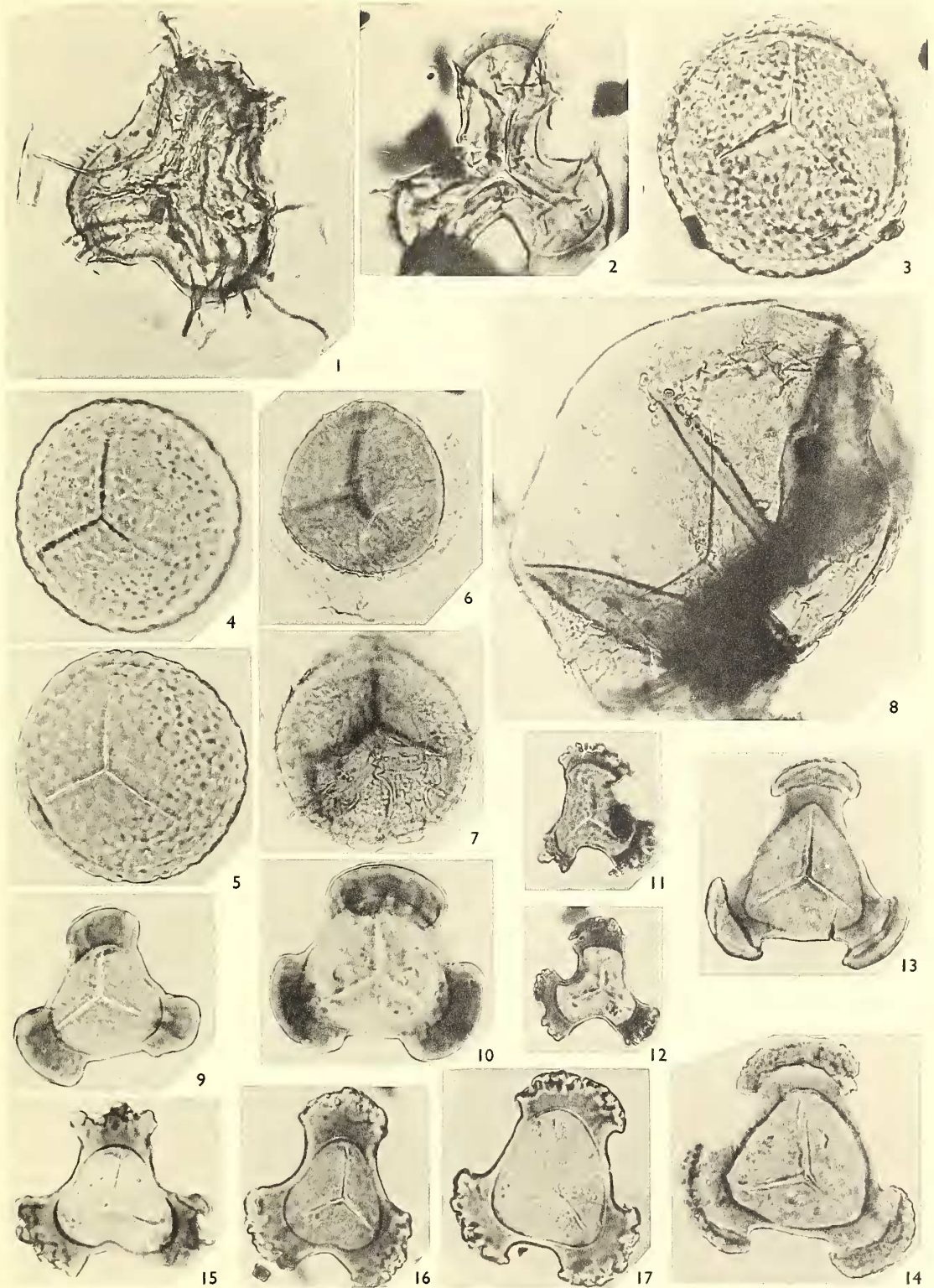
Plate 85, figs. 13, 14

1938 *Zonotrilletes trivalvis* Waltz in Luber and Waltz, pp. 18–19; pl. 4, fig. 41.
 1956 *Triquitrites trivalvis* (Waltz) Potonié and Kremp, p. 88.

EXPLANATION OF PLATE 85

All figures $\times 500$, and from unretouched negatives.

- Figs. 1, 2. *Reticulatisporites?* sp. 1, Distal surface; preparation P145B/43, 39.6 99.0 (L.1052). 2, Proximal surface; preparation P145C/4, 33.2 108.7 (L.1053).
 Figs. 3–5. *Foveosporites insculptus* sp. nov. 3, Proximal surface; preparation P164/6, 20.0 105.0 (L.1055). 4, 5, Holotype; distal and proximal surfaces respectively.
 Figs. 6, 7. *Perotrilites perinatus* Hughes and Playford 1961. 6, Distal surface; preparation P172/3, 44.3 103.8 (L.1057). 7, Distal surface; preparation P163/7, 54.3 101.1 (L.1058).
 Fig. 8. *P. magnus* Hughes and Playford 1961. Proximal surface; preparation M811/2, 56.4 102.4 (L.1258).
 Figs. 9, 10. *Triquitrites batillatus* Hughes and Playford 1961. 9, Proximal surface; preparation P158/7, 25.5 106.2 (L.1062). 10, Proximal surface; preparation P158/7, 27.7 113.0 (L.1061).
 Figs. 11, 12. *Tripartites complanatus* Staplin 1960. 11, Proximal surface; preparation P034/1, 42.7 95.2 (L.1066). 12, Proximal surface; preparation P034/2, 31.3 94.5 (L.1067).
 Figs. 13, 14. *Triquitrites trivalvis* (Waltz) Potonié and Kremp 1956. 13, Proximal surface; preparation P180B/4, 21.0 95.5 (L.1059). 14, Proximal surface; preparation P166/4, 20.6 95.8 (L.1060).
 Figs. 15–17. *Tripartites incisotrilobus* (Naumova) Potonié and Kremp 1956. 15, Proximal surface; preparation P163/10, 34.2 102.1 (L.1064). 16, Proximal surface; preparation P145C/3, 20.9 104.3 (L.1063). 17, Distal surface; preparation P155/3, 37.6 94.0 (L.1065).



PLAYFORD, Lower Carboniferous microspores

